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COMPARATIVE MORPHOLOGY, PHYLOGENY AND CLASSIFICATION OF LAND SNAILS AND SLUGS
(GASTROPODA: PULMONATA: STYLOMMATOPHORA)

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ABSTRACT

The morphologies observed in the pallial complex, digestive tract and central nervous system of numerous stylommatophoran pulmonate gastropod species are described and depicted. It is then possible both to recognize numerous homoplasies in various characters and to arrange the character states in morphoclines, of which the polarity is proposed on the basis of outgroup comparison. Most of the homoplasies are probably convergences related to size, shape, diet or limacization. Some are interpreted as indicating close phyletic relationships. The comparison of a phenetic classification based upon morphological characters suggests that most current, empirical classifications of the Stylommatophora are based upon overall morphological similarity. In the new phylogenetic classification proposed, the order is divided into three supposedly monophyletic suborders: Orthurethra Pilsbry, 1900; Brachynephra *subordo nov.*; and Dolichonephra *subordo nov.* These suborders were probably already differentiated in the Carboniferous.

INTRODUCTION

Among the Gastropoda, the subclass Pulmonata is characterized by the development of a pulmonary cavity that fuses secondarily with the pallial cavity (Fretter, 1975). Three radiations may be recognized: the Archaeopulmonata, which live in marine, littoral environments but include a few terrestrial representatives; the Basommatophora, which live in freshwater; all of the Stylommatophora, under study here, which are terrestrial (Tillier, 1984b). The latter include about 20,500 species (Solem, 1978), and form the richest of the three radiations. Land snails and slugs occur from subpolar to tropical regions, and their local abundance and diversity are a function of climatic stability, at least at lower taxonomic levels (Solem, 1984).

The classification of the suborder Stylommatophora is far from stable. Species are currently grouped into more than 1100 genera that constitute nearly 60 families (1105 genera and 60 families recognized by Zilch, 1960; 56 families recognized by Solem, 1978). Although a general agreement may be found on definition and contents of genera, the rank of suprageneric taxa and the definition of suprafamilial taxa are still under discussion (*e.g.* Solem, 1978; Boss, 1982; Schileyko, 1978a). This relative confusion makes classification of the Stylommatophora a mystery for nonspecialists. At least two reasons may explain, in my opinion, why no systematist of the Stylommatophora can explain how groups should be formed: one is the unrepresentative nature of samples that have been used in attempts to find diagnostic characters; another reason is the nearly total absence of discussions of morphoclines (Maslin, 1952) that link the various character states together in an evolutionary perspective.

Solem (1978) has analyzed the enormous gaps in sampling for characters; in the synthetic volume edited by Fretter and Peake (1975) on functional morphology and physiology of pulmonates, only 25 of the 60 families recognized by Zilch (1960), 53 (4.9%) of the 1105 genera and 47 (0.2%) of the 20500 species are mentioned. Data on transformation sequences in characters are either obviously insufficient (nervous system morphology, histology of genital apparatus and pulmonary complex, shell and radula microstructure), or show so much convergence that the use of corresponding characters has, in most cases, no practical value for recognition of higher taxonomic groups (shell morphology, genital and pulmonary morphology, pallial lobes, etc.). The morphology of the digestive tract, which occupies most of the general cavity, is not even mentioned in any classificatory system (Tillier, 1984a). In the cladistic terminology, one can say that few or no synapomorphies have been recognized: although Pilsbry (e.g. 1900a) explicitly used outgroup comparison to define suborders, groups are currently based on overall similarity of subgroups, and the hierarchy of characters is variable as far as it is defined.

The aim of the present work is to analyze morphological patterns of macroevolution in the Stylommatophora, in order to construct a classification that may be rationally discussed. The work advances in three steps. The first is character analysis and definition of morphoclines. Such an analysis must be based on a sample as representative as possible of all the Stylommatophora, and of their morphological characters. In the earlier parts of this paper, I try to discuss the functional significance of observed character states and to determine the polarity of morphoclines. Evidence for generality of appearance of similar derived character states in different groups is given. The second step is description of families. Character states observed in each family and basic biogeographic data are given in the fifth section. The results of the first sections are used to construct combinations of the most plesiomorphic character states observed in each family, which are thought to represent the closest possible common ancestor of each family. The final step is reconstruction of phylogeny and classification. A phylogenetic reconstruction, taking the frequency of parallel evolution into account, is attempted in the last section. A new classification, based on phylogenetic hypotheses that have not been rejected, is proposed.

METHODS

In order to analyze morphoclines at the suprageneric level, it is necessary to study a sample representative of the various groups of genera. Such a sample can be chosen only within the frame of a preexisting classification. I used as a point of departure Zilch's classification (1960), as partly modified by Solem (Helicarionidae: 1966a; Endodontoidea: 1976, 1982), Breure (Bulimulidae: 1979) and Tillier (Systrophiidae: 1980). I admitted as a postulate that subfamilies recognized by these authors form holophyletic groups. Obviously this monophyly is based on similarity of genera that constitute the various subfamilies; I do not see how one could escape from this approximation, which appeared to be false in a few cases, without restudying representatives of all of the more than 1100 genera. Within this classification, I tried to examine at least one representative of every suprageneric taxon. Only in the beginning of the dissection were several conspecific specimens dissected; afterwards I dissected several conspecific specimens only when the first dissected specimen had some feature looking odd to me. When several species belonging to a single suprageneric taxon were to be examined, I tried to choose them as different as possible on prior data, in order to approach the limits of variation in the taxon under consideration. The choice of species under study was limited by the extinction of a few families and by the absence of material in collections to which I had access.

A total of 243 species, representing 217 genera, 111 subfamilies (of 142) and 51 families (of 60), have been examined (Appendix A). The nine families recognized by Zilch (1960) that are not represented total 34 genera, i.e. about 3% of all genera. Three (representing 12 genera) are extinct and three others are monogeneric (Pleurodiscidae, Otoconchidae, Thyrophorellidae). I considered the Orthalicidae (seven genera) as Bulimulidae, the Trigonochlamydidae (seven genera) as Limacidae, the Aillyidae (one species; Van Mol, 1978) as Helicarionidae, and the Otoconchidae (one genus) as Charopidae, which is an accepted position (Solem, 1978). To my eyes the most important lacuna in the sample is the absence of any of the Megaspiridae: although the family is formed by only five genera, it has an interesting distribution and its position is still problematic (?European Upper Cretaceous-Recent in Brazil and Australia; Pilsbry, 1904).

In the last 20 years, there has been a trend to define and use microscopical characters for classificatory purposes: this has been done by Van Mol (1967) for cerebral ganglia, by Delhaye and Bouillon (1972a, b, c) for the excretory apparatus, and by Visser (1973, 1977, 1981a, b) for the genital apparatus. In my opinion this approach can be successful only if very long-term, because histological techniques are so laborious and time-consuming that the size of the sample examined within a reasonable time is necessarily reduced. Therefore the authors who use microscopical characters are obliged to suppose that characters observed in a very few species are present in large groups, a point which none of them discusses: the use of these characters relies on the underlying assumption that characters are more general when smaller, which seems very questionable. Given the size of the sample under study here, characters used are either macroscopic or visible at magnifications up to 100×. In this order of magnitude accessible characters are those of the morphology of the animal and of its main organ systems: digestive tract, genital apparatus, central nervous system, pallial complex, arterial system. Only characters whose morphoclines seemed well defined at taxonomical levels under study (from the genus to the suborder) were retained: most characters of the external morphology, of the arterial system and of the genital apparatus were eliminated. Another reason for eliminating almost totally external and genital morphologies is that very many more data may be found in the literature on these morphologies than on morphologies of other organ systems, and I preferred to describe and discuss the latter first.

All drawings were made under a camera lucida. In practice the shell of the animals, when present, was first observed and measured (height, diameter, number of whorls) and then cracked or dissolved in acid. The animal without shell was drawn (slugs in dorsal view; axis of flat visceral masses perpendicular to the drawing plane; axis of elongate visceral masses parallel to the drawing plane: Tillier, 1984a). Then the lung roof was removed, spread, and drawn after the lower border of the pneumostome had been cut to allow observation of the anus and ureter opening. After this the rectal and visceral borders of the kidney were cut, the pulmonary kidney wall was folded back upon the pericardium, and the internal kidney morphology was drawn. The animal was then placed again in the same position as in the initial drawing, and the digestive tract was progressively revealed by dissection and drawn before its position within the general cavity was altered by further dissection. Its internal morphology was diagramed in the same drawing. Finally the central nervous system was removed after the nerves and the oesophagus had been cut, and drawn twice in dorsal view: once before, and once after the cerebral commissure had been cut and the cerebral ganglia had been spread on each side of the visceral chain.

Measurements and observations were treated by factor analysis. For each analysis and each variable, the sample was divided into classes of equal effectives, and each modality so defined was treated as an independent variable coded 0 or 1 (matrix written in complete disjunctive form). First, partial analyses were performed by a version of the ANAFAC program (Jambu & Lebeaux, 1979) adapted by Michel Roux and Raymond Baudoin for Apple IIE or IIC microcomputers. Then overall analyses were performed by the ADDAD programs in the CIRCE through the Centre Informatique du Muséum. There is no methodological justification for partial analyses, but only a practical one: the data set is too large to be handled by a microcomputer. Histograms were drawn by a program, written by Raymond Baudoin, which allows the location of every individual, and thus the visualization of the range of every taxonomical group, in the histogram; simplified versions of these histograms are presented below.

The algorithms used for phylogenetic reconstructions are derived from an unpublished work by the late Pierre Delattre, and are described in the final section. The program was written by Raymond Baudoin. Felsenstein's PHYLIP program, version 2.4, was also used.

GENERAL MORPHOLOGY

In all land snails, one can recognize the conical visceral mass, which is coiled into a spiral helix (Thompson, 1917), the epithelium of which secretes the shell; and the foot, which can be retracted into the distal portion of the visceral mass. The coil of the visceral mass is generally dextral, but may be sinistral: where the words right and left are employed below, they must be interchanged to apply to sinistral animals. The pallial border forms the limit between the foot and the visceral mass, and is generally the only part not protected by the shell when the animal is retracted (Solem, Tillier & Mordan, 1984). The pneumostome opens on the right side of the pallial border, in the parieto-palatal angle of the shell aperture (Text-fig. 1). The inferior surface of the foot is the pedal sole, which is used for crawling by means of mucus secreted by the pedal gland, whose opening is situated above the anterior extremity of the pedal sole (mechanism analyzed by Jones, 1973, 1975). The part of the foot anterior to the pallial border is the cephalic region, or head, which bears the invaginable ocular tentacles and rhinophores. The part of the foot posterior to the pallial border is the tail, whose posterior extremity sometimes includes a caudal mucous gland (discussed by Pilsbry, 1896).

In the course of limacization, the number of whorls described by the visceral mass is reduced, the contents of which are incorporated into the foot (Van Mol, 1970; Tillier, 1984a). In semislugs, the distal part of the visceral mass is too reduced to include the whole of the retracted foot, but the stomach is included in the visceral mass, above the pallial border. In full slugs, the visceral mass is still more reduced or absent, and the stomach is included in the pedal cavity. The pallial border extends over the surface of the reduced shell and may cover it totally, forming a dorsal shield (Solem, 1966a); the shell might be absent in full slugs. In the most limacized slugs, the shield itself can hardly be distinguished from the dorsal surface of the foot (Philomycinae, Athoracophoridae, Chlamydephorinae), approaching the structure of an opisthobranch notum.

Size and shape

Size: The largest linear dimension of animals studied here varies between 1.2 and about 140mm, which in first approximation corresponds to a ratio of 1 to 100,000 in volume. One might expect that such a difference in size would be correlated with differences in anatomy, in accord with Galileo's principle of similitude (Thompson, 1917; Lambert & Teissier, 1927). If such correlative variations occur, detecting them in animals partly coiled into a spiral, torted around this spiral and lacking any internal skeleton will be particularly difficult. Insofar as it is admitted that characters used in phylogenetic reconstructions should be functionally independant (Diels, 1921, in Hennig, 1966; Cain, 1982), it is important to detect the extent to which the principle of similitude applies to the morphoclines that are recognized.

Although I did not make statistical tests to check this statement, it seems to me that the relative size of the foot is larger when animals are large; the foot is relatively smaller in small species than in large ones. The principle of similitude may explain this observation: since it is constituted to a large extent by the muscles that move the animal, one can expect that the foot is relatively larger in large animals (problem abundantly illustrated by D'Arcy Thompson, 1917). The same feature may be related to a surface/volume ratio problem (*ibid.*): evaporation from the surface of the foot can be stopped only by retraction of the animal within its shell (Machin, 1975) and is proportional to this surface when the animal protrudes from the shell. Therefore evaporation is more important, relative to the volume of the animal, in a small animal than in a large one, and the only mechanical means to keep the ratio evaporation/volume constant when size diminishes is to reduce the relative size of the foot.

The necessity of avoiding relative increase in the evaporation surface as size decreases also allows one to expect the aperture of small shells to be relatively smaller than that of large shells, because when the animal is retracted into the shell, evaporation occurs from the surface of the animal that remains exposed at the aperture (mantle border or some part of the foot: Solem, Tillier & Mordan, 1984). It seems to me that this is the case, and that the same hypothesis might explain, in possibly a more satisfying way than does the hypothesis of their function as a barrier to predators (Solem, 1966b), why apertural barriers are particularly common in small shells. In Polynesian *Partula*, the surface area of the aperture is correlated with mean rainfall (Emberton, 1982); even in large snails such as New Caledonian *Placostylus*, there is a positive correlation between aridity of environment and development of apertural barriers (Chérel-Mora, 1983).

Slugs have no shell to protect themselves from desiccation, and can use only physiological means and contraction of their foot to limit evaporation from the pedal surface. An indication that these solutions are less efficient for small animals than retracting into a shell may be found in the observation that, in the sample under study here, the smallest slugs are much larger than the smallest snails (ratio of 1 to 5 in maximal length, i.e. about 1 to 125 in volume). However, one should not conclude that slugs can not live in dry environments: a large slug may have a smaller surface/volume ratio than a small snail, and may burrow to escape desiccation and perhaps more easily than a snail, whose shell cannot be deformed. In fact, southern European large parmacellids are found in xeric environments where no snail lives, and it is not absurd to consider that the limiting factor for limacization in xeric environments is not aridity, but rather food supply sufficient for animals large enough to have a favorable surface/volume ratio.

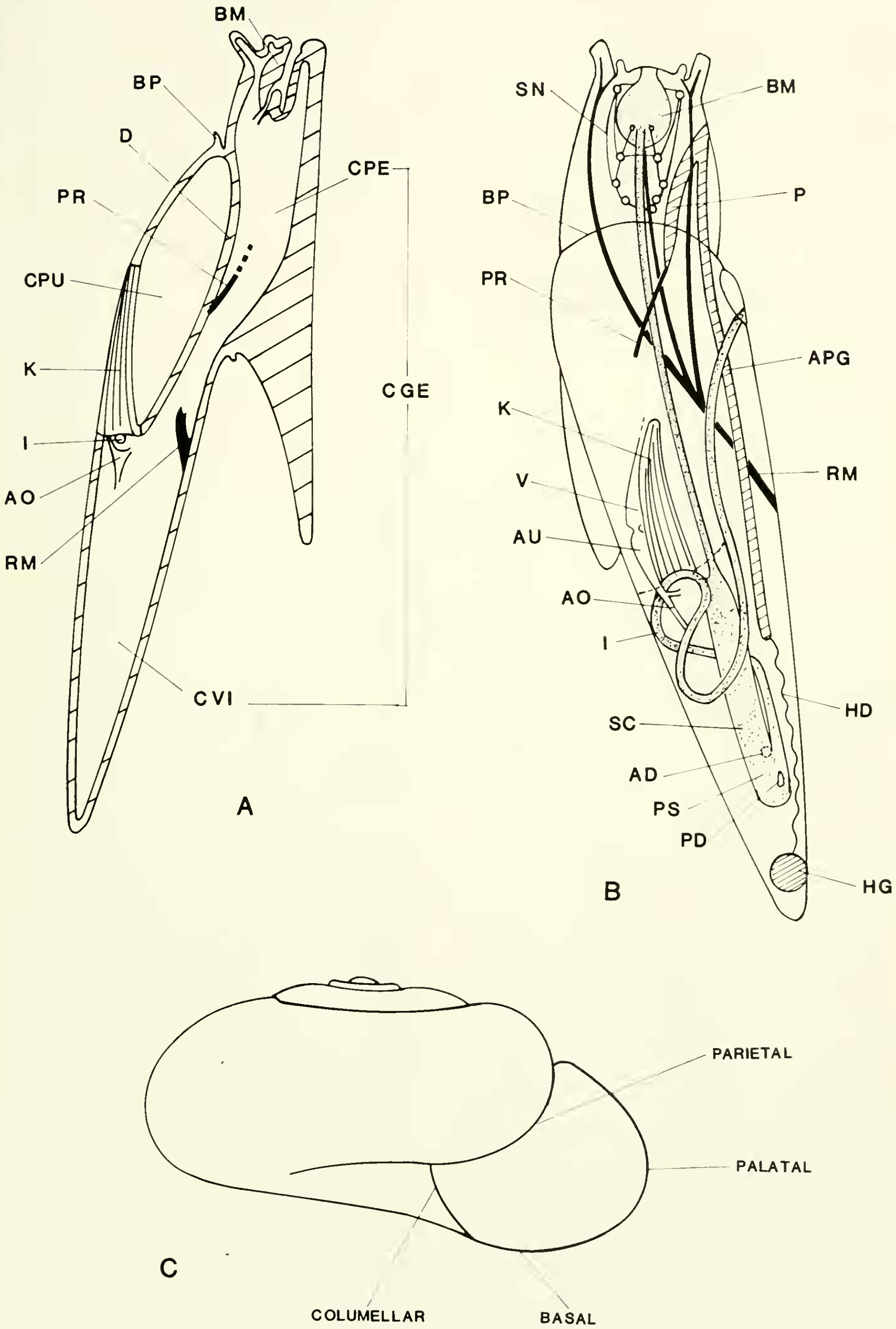
In his discussion of the definition of size parameters of snails, Gould (1969) has shown that at least two linear measurements, height and diameter of the shell, are necessary. He used their sum whereas other authors used their product (Tillier, 1981; Chérel-Mora, 1983). In these cases, the shape was reasonably constant within each group under study. Here we deal with snails, semislugs and slugs exhibiting a large range of shapes. Consequently the various snails and slugs under study were arranged following their apparent size from 1 to 236 (snails without shell; specimens belonging to seven species were no longer available when this was done), and their rank was used as a statistical parameter (Appendix B). Approximate measurements of the volume of 40 specimens without shell showed that the rank so determined is an increasing function of the volume of the animals.

Shape: It is equally important to detect correlations between the shape of the animals and character states: I showed elsewhere (Tillier, 1983, 1984a, 1984b) that some character states used as synapomorphies of orders are only the most apomorphic states of morphoclines related to limacization. Likewise, the important variations occurring in the

TEXT-FIG. 1. Plan of organization of the Stylommatophora. 1A, sagittal section; 1B, dorsal view; 1C, shell and terminology of the various regions of the apertural border, of which the growth generates the corresponding areas of the shell.

The visceral mass has been drawn uncoiled, which is biological nonsense, for asymmetry, torsion and coiling result from a single cause, differential growth of the visceral mass.

AD, opening of anterior duct of digestive gland; AO, aorta; APG, hermaphrodite portion of genital apparatus; AU, auricle; BM, buccal mass; BP, pallial border; CGE, general cavity; CPE, pedal cavity; CPU, pulmonary cavity; CVI, visceral cavity; D, diaphragm; HD, hermaphrodite duct; HG, hermaphrodite gland; I, intestine; K, kidney; PR, penial retractor muscle; PD, opening of posterior duct of digestive gland; PS, gastric pouch; RM, free retractor muscles; SC, gastric crop; SN, nervous system; V, ventricle.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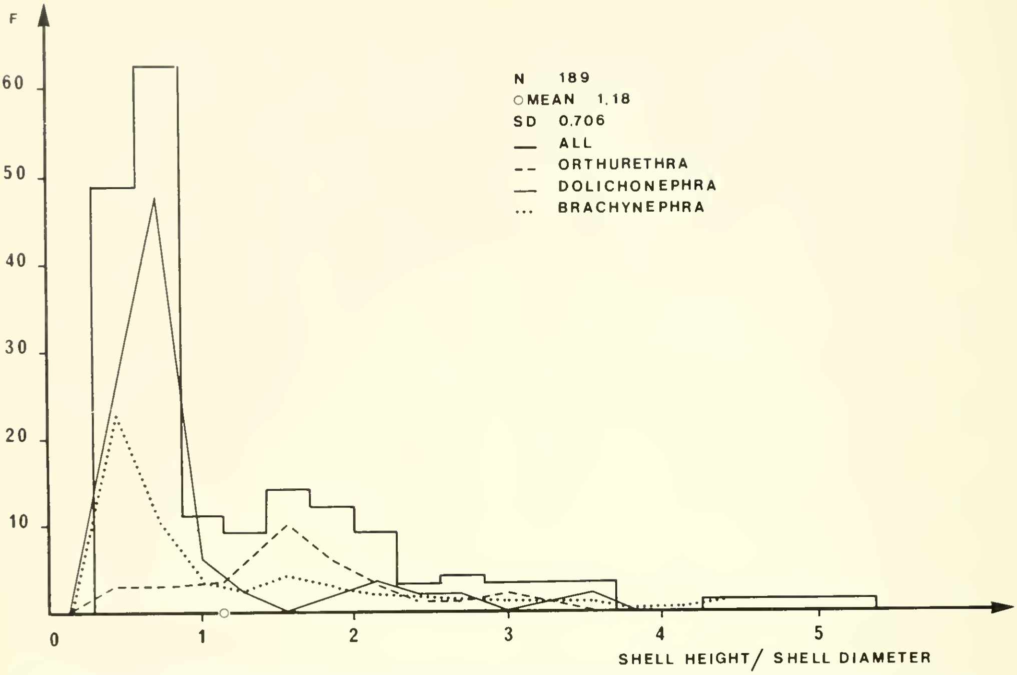


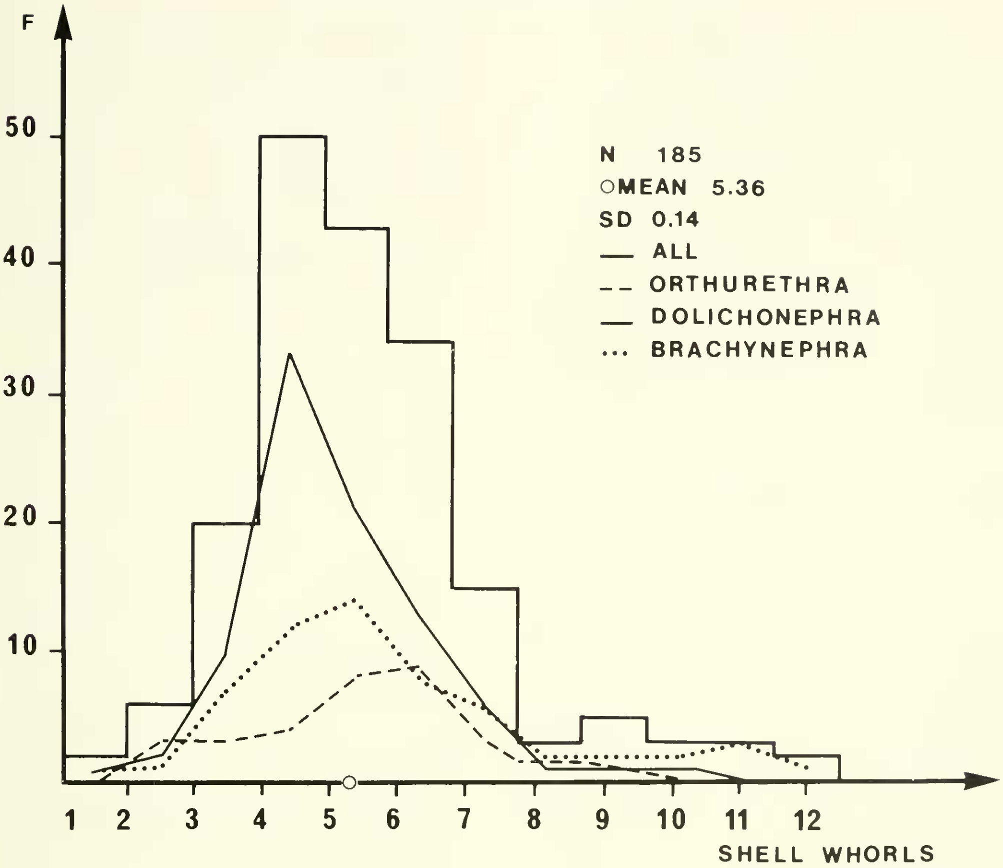
TEXT-FIG. 2. Shell shape of snail and semislug species studied (ratio shell height/shell diameter; data, Appendix B). Suborders Brachynephra and Dolichonephra defined in last section.

shape of visceral mass of snails can be correlated with anatomical character states that could be interpreted as bringing additional information to bear on phylogenetic relationships. Furthermore, recent works by Cain (1977, 1978a, b, 1980, 1981), Chérel-Mora (1983), Emberton (1982), and Tillier (1981) tend to show that shell shape has an important adaptive value at the level of the guild of terrestrial gastropods.

As noticed by D'Arcy Thompson himself (1917: 515), his work on modelling of gastropod shell shapes is useless for analyzing the internal variations related to variations in external shape: his models, like those of Raup (1966), describe only surfaces. To analyze the internal variations related to variations in shape, we should define a system of coordinates within the cone representing the visceral mass, and study the deformations of this system when this cone is coiled into a spiral helix whose height and diameter vary. Being unable to build such a model, I used the ratio, height of shell/diameter, to define the shape of the visceral mass, as done by Solem (1966b), Cain (*op. cit.*) and others (Appendix B). Shapes can be compared precisely by this ratio only if they are similar, which is not the case here where such a gross approximation must be compensated by wide classes. In Appendix B, the shape of semislugs is represented by the number 1000 and the shape of slugs is represented by the number 2000.

The histogram of snail shell shapes (189 species; Text-fig. 2) exhibits for all Stylommatophora the bimodality already discussed by Cain (*op. cit.*) for various faunas: average shapes (H/D ≅ 1.18) are less represented than elongate and flat shapes.

The number of whorls of the visceral mass within the shell is another important shape parameter, which is independent of size. When low, it constitutes an index of the degree of limacization. Generally the viscera do not fill the shell cavity up to its top. In most cases, the apical portion of the shell cavity is filled with mucus-like matter in alcohol-preserved specimens. Comparison of the histograms (Text-figs. 3,4) shows that there is seemingly no simple relationship between the number of whorls of the shell and the number of whorls of the visceral mass (Appendix B). Although in general the length of the visceral mass increases with the length of the shell (in whorls), the number of whorls in a shell does not allow one to predict the number of whorls in



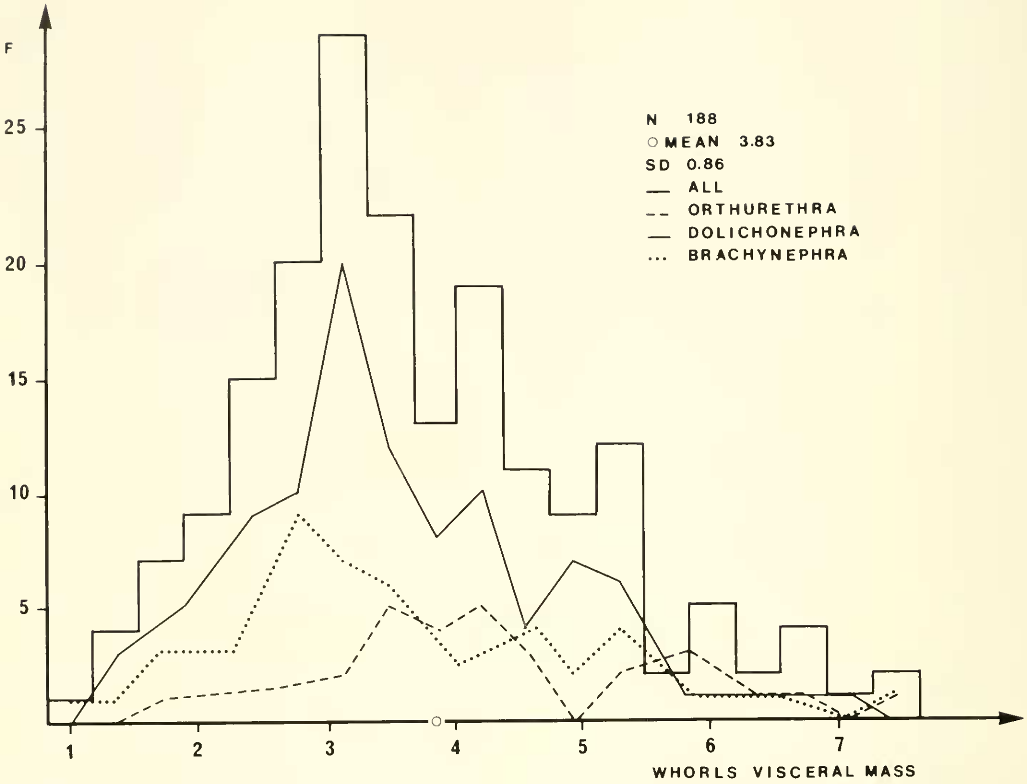
TEXT-FIG. 3. Whorl number of shells of the snail and semislug species studied (data, Appendix B).

the corresponding visceral mass. Intraspecific variation in visceral mass whorl number is relatively important (studied in only one genus, the New Caledonian charopid genus *Pararhytida:* Tillier & Mordan, 1986). I must suppose that the size of the sample divided into broad classes eliminates the effects of this variability in the statistical analyses of morphological characters.

External morphology of foot

Proportions: Observation of stylommatophorans alive shows that the proportions of the foot do not vary by chance more than relative foot size. In order to discuss these variations, it is necessary to distinguish between aulacopod feet, surrounded by a well-defined suprapedal groove, and holopod feet, which lack such a groove (Pilsbry, 1896). As stated by Solem (1978), "the basic distinction seems a real one"; but in my opinion it is not possible to use aulacopody as a synapomorphy before its biological meaning and other characters of the group which its presence defines (Aulacopoda Pilsbry, 1896; Solem, 1978) have been discussed.

In the Stylommatophora, width of the pedal sole is generally greater in proportion to sole length in large animals than in small ones. This feature might correspond to the maximization of the surface used for creeping, which allows the animal to keep the ratio of the surface of the pedal sole to the weight of the animal nearly constant as size increases: this feature is reminiscent of the relatively large diameter of the bones in the legs of large tetrapods, discussed by Galileo long ago. For the same size, holopod feet are relatively wider than aulacopod feet. This difference in pedal sole shape seems to be related to differences in body shape of animals that exploit



TEXT-FIG. 4. Length in whorls of visceral mass of snails and semislugs studied (data, Appendix B).

vertical or oblique surfaces. It has been noticed that there is a correlation between elongation of the shell and exploitation of such surfaces (Cain & Cowie, 1978; Cameron, 1978, 1981; Cook & Jaffar, 1984); but no author noticed that all the animals seen to have such a correlation also have a holopod foot, probably because in the Northern Hemisphere there are very few animals with an aulacopod foot, which exploit vertical or oblique surfaces. In Africa, Southeast Asia and the Pacific Islands, many arboreal or semi-arboreal aulacopod snails are helicarionids and endodontoids. The shell of these is not elongate as in most holopod species that exploit vertical or oblique surfaces, but the proportions of the foot are different: in most arboreal aulacopod snails that I have observed, the head is clearly shorter than the tail and the foot is especially narrow, whereas the foot of related snails that live in the same forests at ground level has more usual proportions, i.e. it is wider and the head is about as long as the tail.

Snails whose head is clearly longer than the tail are not common. As noted by Watson (1915), the most evident functional explanation for such proportions is aptitude for carnivory, which involves a large buccal mass and consequently a large pedal cavity and a long head (Rhytididae and Oleacinidae, but no observed Streptaxidae, in which the great length of the lung allows housing of the buccal mass in the lower part of the visceral cavity).

Interpretation of aulacopod condition: Although the aulacopod condition is used as a synapomorphy in the Pilsbry-Baker system, no interpretation of its origin has been proposed (Watson, 1920; Wächtler, 1935; Baker, 1955; Solem, 1978). The distinction between aulacopod and holopod morphologies is often not very clear-cut (Solem, 1978). With a few exceptions (Pilsbry, 1946), the distinction is easy in groups placed by Solem (1978) either in the Holopoda or in the Aulacopoda. But, as noticed by Solem himself, an aulacopod or quasi-aulacopod condition might occur not only in some representatives of most groups of the Holopodopes *sensu* Solem (Ferussaciidae, Subulinidae, Spiraxinae, Streptaxidae, Systrophiidae), but even in some Mesurethra *sensu* Solem (some Clausiliidae).

In nearly all species with an aulacopod foot, whether belonging to the Aulacopoda *sensu* Solem (endodontoids excepted), shell growth is indefinite: passage to the adult stage, indicated by maturation of the genital apparatus, is not marked by any change in the growth of the shell, the border of which remains sharp and unexpanded. On the other hand, shell growth is definite in nearly all animals having a holopod foot, including the Holopoda *sensu* Solem: as the genital apparatus reaches maturity, the orientation in growth of the last whorl is often modified and the apertural border is thickened or expanded. Finally in the few cases (about ten) in which I could observe well-developed embryos or newly born juveniles of orthurethran and holopod species (*sensu* Solem, 1978), their foot was distinctly aulacopod. From these three sets of observations, I propose the following hypotheses: first, the aulacopod morphology is a character of juvenile stylommatophorans; second, in groups in which adult animals have an aulacopod foot, the aulacopody is a paedomorphosis that might be regarded as neoteny (retardation) in the sense defined by Gould (1977): the absence of an adult morphology in the shell of aulacopod animals indicates that everything seems as if most aulacopod snails continue in the juvenile mode of growth until after sexual maturity has been attained.

However, this paedomorphosis in foot and shell morphology occurs to a variable extent: in some groups, an aulacopod foot is associated with a shell with definite growth (e.g. some *Trochomorpha* with an expanded aperture, endodontoids) and in some other groups, a holopod foot is associated with indefinite shell growth (e.g. *Achatina fulica*). This shows, at least as far as the hypothesis of the paedomorphic origin of aulacopody is true, that paedomorphosis may be affected by mosaic evolution and is not necessarily effective for all organs of an organism; a point that is confirmed by the observation of a paedomorphic morphology in the digestive tract of snails whose other characters exhibit adult morphology (*Vallonia*, *Zonitoides* described below). As stated by Delsol and Flatin (1979), paedomorphosis should be discussed character by character.

Internal anatomy

Description: Two principal cavities, the pulmonary and the general, may be distinguished in land snails. During ontogeny, the pulmonary cavity forms by invagination of the mantle border, which secondarily fuses with the pallial cavity, which is homologous with the prosobranch pallial cavity, the latter forming the pneumostome region (Regondaud, 1964; Fretter, 1975; Tillier, 1984b). The heart and kidney form the proximal part of the lung roof, and the whole system is called the pallial complex or pulmonary complex. The general cavity contains the digestive tract, central nervous system, arterial system and free retractor muscles (Text-fig. 1). For convenience in description, I shall distinguish within the general cavity the pedal cavity, extending from the anterior extremity of the foot to the level of the pallial border, and the visceral cavity, which occupies all the visceral mass except the lung cavity. This distinction is purely formal, for the same organ systems extend without any discontinuity from the pedal cavity into the visceral cavity. The pedal cavity does not extend into the tail of snails as it does in slugs, of which the visceral mass is included in the foot. In such slugs the visceral cavity, pedal cavity and general cavity are indistinguishable (Van Mol, 1970, 1971; Tillier, 1984a).

The arrangement of the digestive tract, the object of incredibly few descriptions, has been discussed elsewhere (Tillier, 1984a). The oesophagus (OE, Text-fig. 1, Figs.) opens dorsally from the anterior buccal mass (BM). Its internal ornamentation, if present, consists in longitudinal ridges. The oesophagus might be partly differentiated into an inflated oesophageal crop (OC, Figs.); but, contrary to the statement of most treatises of zoology (e.g. Franc, 1968), many stylommatophoran species do not have an oesophageal crop (Figs.). Two salivary glands (SG) are appressed to the oesophagus. They comprise numerous acini whose ducts converge into two main salivary ducts, which open into the buccal cavity on each side of the oesophageal opening. The oesophagus runs backward along the parietal side of the visceral cavity, and most generally expands into a gastric crop (SC) a short distance above the top of the lung. The most common internal ornamentation of the gastric crop, if present, consists of two ventral ridges that delimit a groove; more longitudinal ridges might be present. The gastric crop is prolonged by the caecum of the gastric pouch (PS), from which the intestine (I) runs forward and ventrally. The anterior duct of the digestive gland (AD) opens into the concavity of the gastric pouch, between the openings of the gastric crop and proximal intestine. The posterior duct of the digestive gland (PD) generally opens through the parietal wall of the gastric pouch. When present, the ventral groove of the gastric crop leads to the opening of the anterior duct, from which one usually short typhlosole emerges into the proximal intestine. A second, longer typhlosole, issuing from the opening of the posterior duct, runs parallel to the first one into the proximal intestine and reaches at most the beginning of the periaortic intestinal loop. A ridge might join the openings of the ducts of the digestive gland and with the proximal portions of the typhlosoles delimit a curvilinear triangle on the parietal wall of the gastric pouch. The arrangement, length and thickness of these ridges are variable even within a single family. The intestine runs forward along the columellar side of the visceral mass, turns to the left under the anterior gastric crop or the posterior oesophagus, turns around the aorta clockwise in dorsal view (periaortic bend) before turning forward again (prerectal bend). The rectum runs along the suture from the summit of the lung to the roof of the pneumostome.

The genital apparatus will be much less discussed here than other systems (Duncan, 1975). The common genital orifice opens on the right side of the head. The hermaphrodite branch runs along the parietal side of the visceral mass to a point above the stomach, where the hermaphrodite gland, formed by one or several clumps of acini, is embedded in the upper lobe of the digestive gland (HG, Text-fig. 1). Above the lung, the albumen gland either spreads between intestinal loops distal to the gastric crop (Orthurethra, Aulacopoda *sensu* Solem, 1978), or spreads appressed along the gastric crop (most Holopoda *sensu* Solem, 1978). When very long, the spermathecal stalk turns to the left along the periaortic intestinal bend at the level of the summit of the lung, and the spermathecal head lies appressed beneath the pericardium on the left side of the aorta. In large species, the vagina is attached to the pedal wall by very short muscles. Exceptionally, one branch of the free retractors might insert on the atrium or close to the base of the spermatheca (Tillier & Mordan, 1986). The penis connects the hermaphrodite branch of the genital apparatus into a genital atrium close to the genital orifice, and is generally attached by a penial retractor muscle (PR) to either the lung floor (= diaphragm) or the stem of the free retractor muscles.

The central nervous system (SN, Text-fig. 1) is always entirely contained in the pedal cavity in the Stylommatophora. It is formed by two dorsal cerebral ganglia (CG, Figs.) connected by cerebral commissure (CC) above the digestive tract, two latero-ventral pleural ganglia (PLD, PLG) connected by a visceral chain of ganglia beneath the digestive tract, and two ventral pedal ganglia (PG). The visceral chain comprises two parietal ganglia (PAG, PAD) and one median visceral ganglion (VG). The cerebro-buccal connectives join the lower surface of the cerebral ganglia to the buccal ganglia, which are appressed to the buccal mass on each side and below the origin of the oesophagus.

The free retractor muscular system (RM, Text-fig. 1, Figs.) is made of branches of the columellar retractor. The latter is inserted on the inner shell surface along the columella; this insertion is the only fixed point in the system formed by the animal and its shell. As may be expected from the principle of similitude, the free retractor system is more developed in large animals; the lateral pedal retractors in particular are very important in large snails such as *Helix pomatia* (Jones, 1975: Fig. 1) and are absent from small species. Other free retractors are the buccal retractor muscle, distally divided into at least two branches inserted under the buccal mass, and the ocular retractors, distally divided into ocular and rhinophoral branches. In all cases the free retractor system passes along the right side and beneath other organ systems in the pedal cavity, the genital apparatus excepted. The latter, penis excepted, lies on the right side and beneath the free retractor system, and the right ocular retractor generally passes between the penis and vagina. This general pattern varies, particularly with taxonomic position and degree of limacization (Solem, 1978; Tillier, 1984a). My impression, based on dissection of several hundred taxa, is that the free retractor system might be useful for comparison of closely related genera (Wurtz, 1955), but that convergence is far too common for it to provide useful data in an analysis of morphoclines at familial or suprafamilial levels.

The principal branches of the arterial system are remarkably constant in their arrangement (Duval & Runham, 1981). The cephalic aorta is often appressed to the underside of the diaphragm in large snails, but never in slugs.

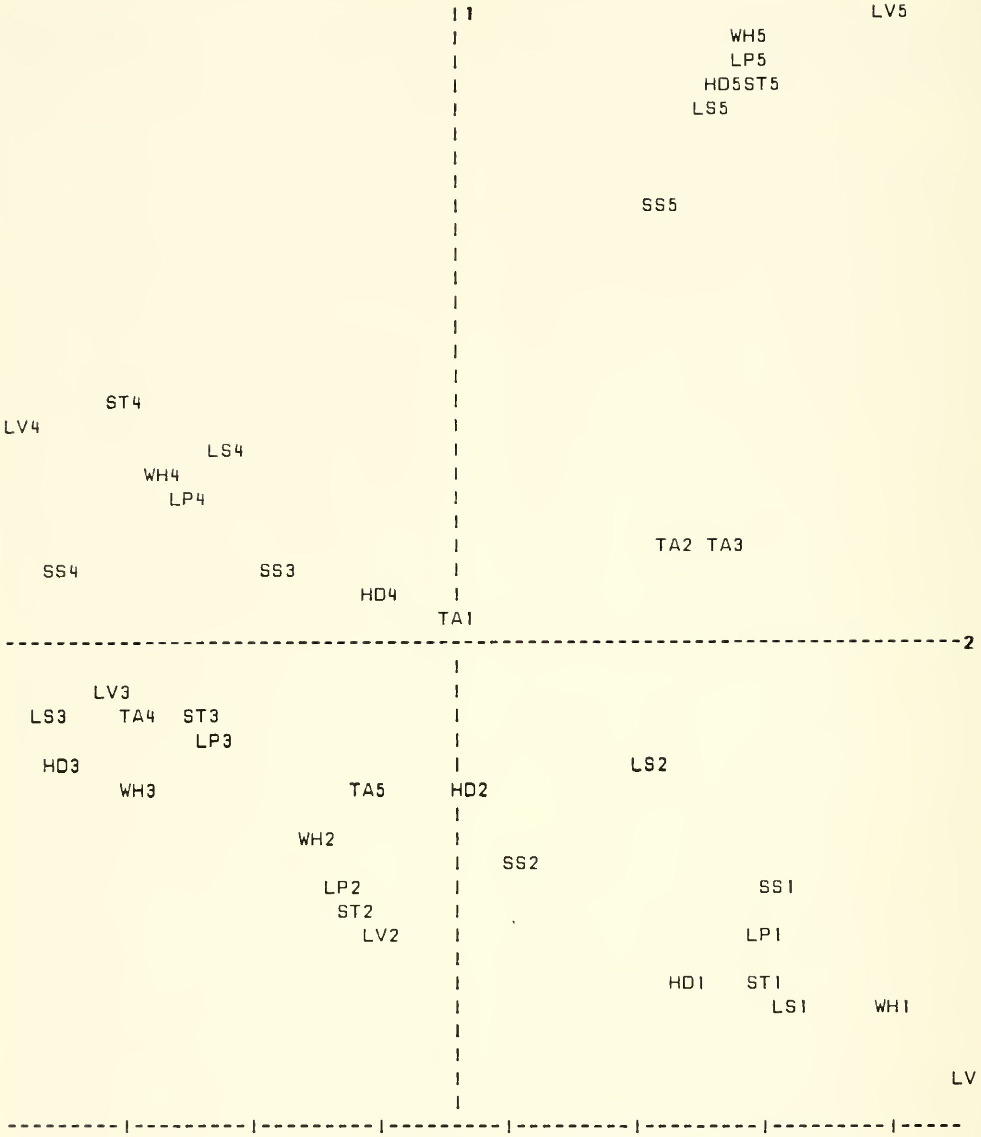
Relative positions of organ systems: The relative positions of the various organ systems and of the pulmonary complex must be kept in mind, in order to understand some of the constraints on anatomical transformations and relative movements during contraction within the shell. There are some anatomical constraints (Text-fig. 1). First, the central nervous system surrounds the oesophagus, which limits nervous concentration: the latter limits food size, which seems surprising to vertebrates like us. Second, the aorta must cross the periaortic bend of the intestine: some *a priori* bizarre arrangements in the digestive or arterial systems of some slugs and semislugs may result directly from this constraint (Tillier, 1984a; Testacellinae: Lacaze-Duthiers, 1887; Chlamydephorinae: Watson, 1915). Third, the position of every organ system relative to the others is generally fixed by two points on the surface of the general cavity (genital orifice and penial retractor insertion for genital apparatus, free muscle insertions, mouth and anus for digestive tract, etc.). Topological transformations of the organs are possible only to the extent that two portions of organs between two fixed points do not overlap. For example, the relative position of the penis is quite constant when a penial retractor is present (succineids and snails having a free right ocular retractor excepted); but the relative position of the rest of the genital apparatus, which is fixed only by the genital orifice and the genital branch of the aorta, may vary greatly in slugs: on the right side of the digestive tract in the Helicarionidae, on the left and underneath in *Arion,* above in *Omalonyx,* etc.

It is equally important to distinguish fixed from mobile parts in the movements of the animals. Fixed parts are all those that are proximal to the tops of the lung and the columellar retractor. Indeed, there is no muscle that would allow movements of the proximal part of the visceral mass within the shell; if such movements occur, they are provoked only by a violent retraction of the foot or by variations in hydrostatic pressure, but they do not affect the relative positions of the organs. This fact allows us to use measurements of the various organs above the lung, at least for a variation that was analyzed in only one genus (*Pararhytida:* Tillier & Mordan, 1986): distance from the top of the lung to the top of the stomach, length occupied by intestinal loops, length of the part of the visceral mass above stomach (Appendix B). These lengths have been measured in whorls, in order to have measurements that are independent of size.

When a snail retracts within its shell, the ocular tentacles and rhinophores are first invaginated. Then the buccal mass is pulled backward by the buccal retractors, whose contraction invaginates the anterior part of the head. Next, pedal retractors, when present, contract progressively backwards. When retraction is achieved, the head is totally invaginated and the tail is generally proximal to the pallial border (Solem, Tillier & Mordan, 1984). All organs between the mouth and the top of the lung are folded, or translated into a space formerly occupied by the lung cavity, by means of the expansion of the diaphragm. The lung roof may be folded (by retraction of the columellar muscle?), but seemingly not contracted (no intrinsic muscles), such that the pallial border is translated as far as possible from the shell aperture. When the nerve ring is wide enough, as is usual, the buccal mass slides backwards through the ring; when the nerve ring is too narrow, the buccal mass is pulled back above the nerve ring, by means of sliding of the oesophagus forward through the ring (observed in the Partulidae).

Proportions in visceral mass: Only snails have been treated because it is not possible to take the same characters into account in snails and slugs. The data set being incomplete for all species, 159 species have been treated. For each species, available data are: size rank (TA); shape (HD = shell height/shell diameter); number of whorls of the shell (WH) and visceral mass measurements. The latter are lengths in whorls: length of the lung from pneumostome to top of the lung along the rectum (LP); length between the top of the lung and the top of the stomach (LS); length of the upper lobe of the digestive gland between the top of the stomach and the top of the spire (SS); and length of the stomach plus gastric crop (ST), the foremost part of the latter being in a few cases at the level of the lung cavity (Appendix B).

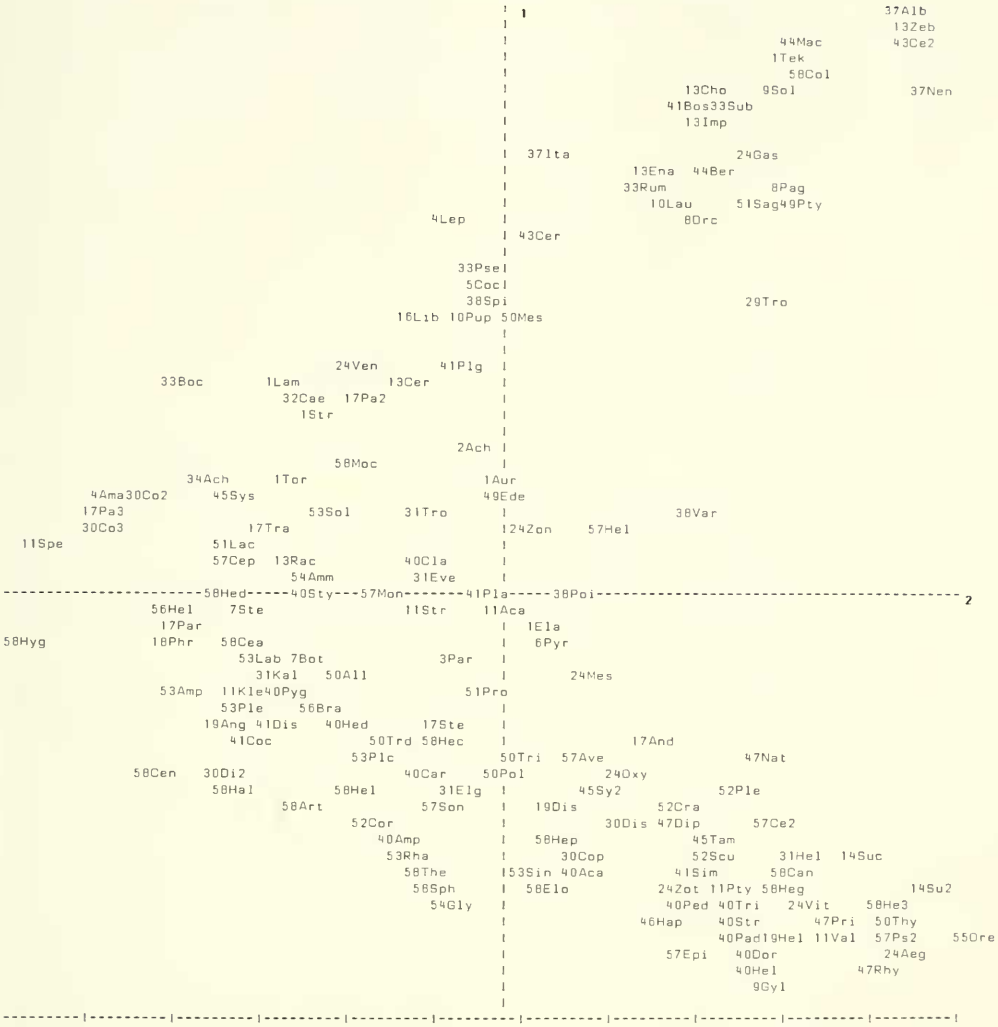
For each parameter the sample has been divided into five classes including equal numbers of species, and the table has been written in complete disjunctive form (limits of the



TEXT-FIG. 5. Factor map of correspondences among characters of visceral mass. Plane (1,2). Data, Appendix B, limits of the classes, Appendix C.

classes, Appendix C). Each class is numbered from 1 to 5 in increasing value of the variable considered. The results of the analysis are represented Text-fig. 5 (modalities, plane 2,1), Text-fig. 6 (individuals, plane 2,1) and Text-fig. 7 (individuals, plane 3,1).

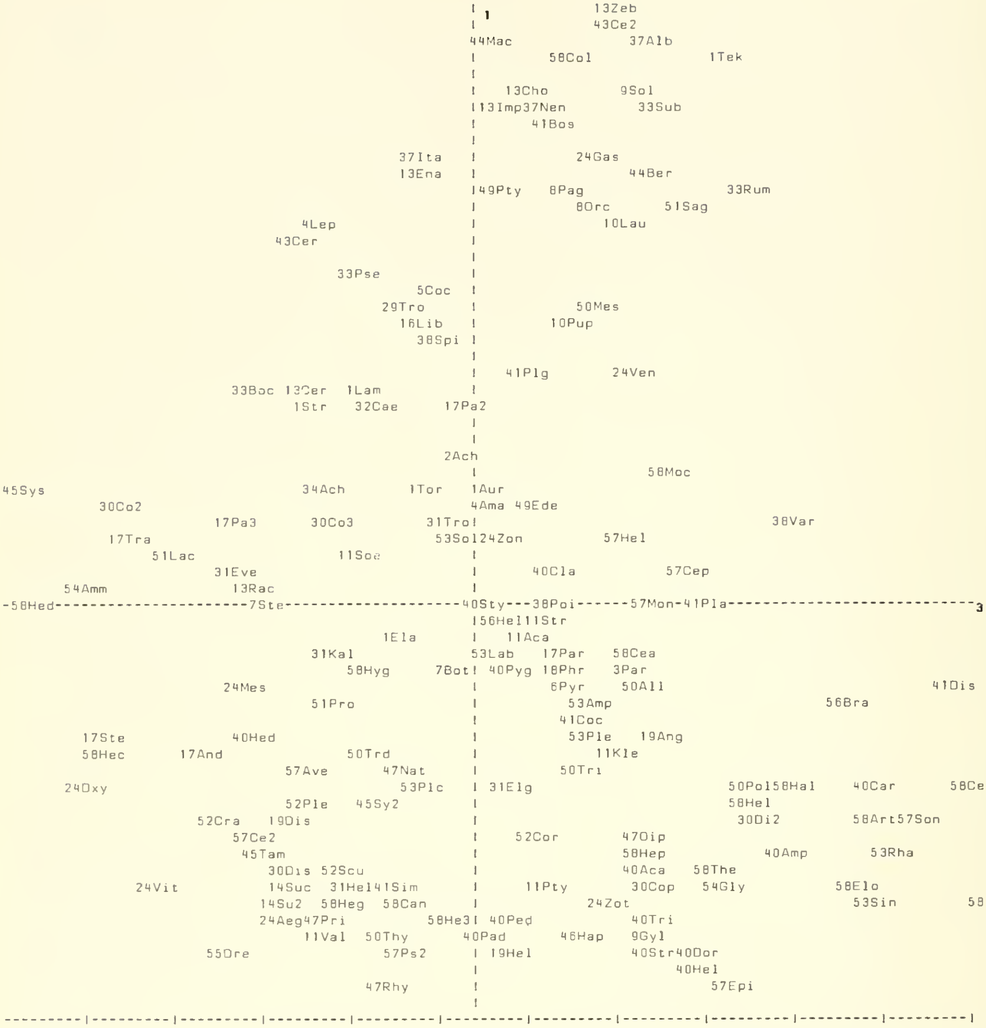
Text-figure 5 clearly shows an overall correlation among lengths of the lung, stomach and upper part of the visceral mass, and shape of the shell (= shape of the visceral mass): value-clusters of various characters follow one another along the first axis, and axis 2 separates very flat and very elongate shells (on the right) from average-shaped shells (on the left). This general correlation is independent of the systematic position of the animals (Text-fig. 6). Indeed, species are arranged in Text-figs. 6 and 7 by their shapes, not their taxonomical suprageneric affinities. This means that the proportions of the various



TEXT-FIG. 6. Factor map of correspondences among individuals for characters of visceral mass. Plane (1,2). Abbreviations, Appendix A; data, Appendix B; limits of classes, Appendix C.

parts of the visceral mass of stylommatophorans are fairly constant. Indeed, if one stretches a flat visceral mass into an elongate one, the length of every part measured in whorls would increase. This is exactly what is shown in Text-fig. 5, where modalities representing the lengths in whorls and those representing shapes correlatively follow one another.

The proportions in the visceral mass that correspond to this overall correlation have probably no taxonomical or phylogenetic value within the Stylommatophora, although they might represent a synapomorphy of the Stylommatophora within gastropods (not checked here). On the other hand, character states that significantly modify the position of a taxon with respect to shape should be examined and discussed. In such cases the problem is to determine whether these character states are synapomorphic at the familial level, or at some lower level not considered here. One example is the position of *Trochomorpha* (29Tro) in Text-figs. 6 and 7, not associated with the corresponding shape; since only one trochomorphid species was exam-



TEXT-FIG. 7. Factor map of correspondences among individuals for characters of visceral mass. Plane (1,3). Abbreviations, Appendix A; data, Appendix B; limits of classes, Appendix C.

ined, no use can be made of the resulting proportions.

In some other cases, the seemingly aberrant position of some taxa is probably related to the fact that the H/D ratio does not take into account all shape parameters. For example, the position of succineid (14Su1, 14Su2) and oleacinid (38) snails in Text-figs. 6 and 7, close to shapes much flatter than theirs, may be related to the rapid increase of the whorls: their last whorls occupy relatively much more of the total volume of the animal than in other snails with the same H/D ratio and whorl number, and their organs are relatively shorter in whorl length. To find such taxa aggregating with those of similar shape, I should probably have introduced a variable for increase in diameter of the cone formed by the visceral mass (e.g. the ratio of shell diameters from one whorl to the next).

Unlike shapes, sizes show very weak correlations, if any, with other modalities taken into account in the analysis (Text-fig. 5). Very small sizes (TA1) do not contribute at all to the first five axes. In other terms, miniaturization (or size increase, if the ancestral snails were small) has no influence on proportions of the visceral mass. This is true not only overall, but often also locally, as may be seen by comparing the drawings of the visceral masses of two species of *Helicopsis* (Figs. 665, 671) of which shell diameter varies from 1.5 to 7mm. The contribution of other size modalities is also extremely weak, and their absolute contribution to the first axis is nil.

It might be concluded that, to a first approximation, the principle of similitude does not apply to the proportions of the visceral mass of snails. This is surprising particularly regarding the lung, whose length should increase with size at constant shape in order to maintain the ratio of respiratory surface/total volume constant. It might be supposed that diminution of this ratio as size increases is compensated by physiological mechanisms, but I do not believe so because congeneric species of various sizes, whose physiological mechanisms are probably very similar, have the same lung length (e.g. *Helicopsis*). It might be concluded that the respiratory surface is not the functional limiting factor for lung surface decrease. This point is confirmed by the important decrease of the pulmonary surface, without any other apparent change, observed in the Helicarionidae (Figs. 296–340) and other semislugs. Such a limiting factor may be either the necessity for retracting the foot into the volume of the lung cavity, if retraction is the only way to limit evaporation from the pedal surface; or the necessity for a long ureteric groove, if there is no closed ureter (*v. infra*).

The absence of variations in the proportions of the visceral parts of the digestive tract, intestine excepted (*v. infra*), is less surprising. The relative diminution in size of the stomach and gastric crop as size increases might be counterbalanced by the development of an oesophageal crop (*v. infra*). The relative diminution of the digestive surface might be counterbalanced by an increase in the number of lobules of the digestive gland, as in the case of the alveoli of vertebrate lungs (not checked here).

PULMONARY COMPLEX

Following principally the work of Semper and Simroth (1894), Pilsbry (1900a, b) proposed to distinguish suborders in the Stylommatophora by the morphology of their excretory system, and chiefly by the degree of closure of the ureter. He defined the orthurethran kidney, long and without any ureteric tube, as the diagnostic character of the Orthurethra; the heterurethran kidney, transverse and prolonged by a ureteric tube, as diagnostic of the Heterurethra; and the sigmurethran kidney, shorter than the orthurethran one and prolonged by a ureteric tube, as diagnostic of the Sigmurethra. The formerly-introduced Aulacopoda (Pilsbry, 1896), whose morphology is discussed above, became a division of the last group. In 1955, Baker defined the mesurethran kidney as non-orthurethran but lacking a ureteric tube, and characteristic of the suborder Mesurethra. These characters have been discussed by Watson (1920) and the corresponding suborders have been accepted by Baker (1955), Solem (1978), Zilch (1959–1960) and Boss (1982). Wächtler (1934) insisted on the occurrence of intermediate morphologies and recommended the rejection of the taxonomic use of these characters, whereas Schileyko (1978a, b) accepted only the first of the divisions proposed by Pilsbry between the Orthurethra and the non-Orthurethra.

The microscopic structure and ultrastructure of the kidney and ureter have been studied by Bouillon (1960), and Delhaye and Bouillon (1972a, b, c), but in a sample obviously too small: the ultrastructure was discussed only in helicids and the microscopical structure was described in only seven stylommatophoran species belonging to seven of the 60 families recognized by Zilch (1960). The function of the kidney and lung have been surveyed by Machin (1975) and Ghiretti and Ghiretti-Magaldi (1975).

The absence of any retrograde ureteric tube is probably plesiomorphic, as implicitly or explicitly expressed by all authors since Pilsbry (1900a) who have discussed kidney organization: no prosobranchs, no opisthobranchs and few archaeopulmonates and basommatophorans exhibit such a structure (Fretter & Graham, 1962; Gosliner, 1981; Hubendick, 1978).

Morphological characters

General description, function: The pulmonary, or pallial, complex forms the parietal and basal parts of the visceral mass of snails, from the pallial border to the periaortic intestinal bend (Text-fig. 1). It is composed of the walls of the lung cavity, kidney and heart. The lung cavity is generally considered not homologous with the pallial cavity of other gastropods, which forms only the pneumostome region as noted above (Régondaud, 1964; Fretter, 1975).

The lung roof is applied to the parietal and basal walls of the shell. The rectum, which runs along the suture, forms its right border, and a branch of the columellar muscle forms its left border. The lung cavity is distally limited by the pallial border, and opens to the outside through the pneumostome, which is adjacent to the anus. The kidney is proximal, on the left side of the lung roof. Its shape is approximately triangular: its visceral side runs along the periaortic intestinal bend; its rectal side runs parallel to the rectum; and the pericardium is applied to its pericardial side, opposite the rectum. The pericardium is prolonged toward the pallial border by the pulmonary venous system, and toward the visceral cavity, outside the lung cavity, by the aorta, which crosses the intestinal bend in the concavity of the latter before dividing into an anterior and a posterior branch. The ureter (ureteric zone, ureteric groove or ureteric tube) runs backwards from the renal pore, which is usually at the recto-pericardial summit of the kidney, along the rectal side of the kidney to the top of lung cavity, and turns forward to the pneumostome along the rectum. The opening of a ureteric tube, which always originates from the kidney pore, can be at any distance from the kidney pore, and on the dorsal side of the pneumostome when sigmurethry is achieved. The lung cavity is separated from the visceral cavity by the lung floor, or diaphragm, which generally has transverse muscular fibres. In large species, the anterior branch of the aorta is partly fused to the diaphragm, distal to its circuit of the intestine. The pallial border includes a glandular formation that spreads either between the rectum and ureter (*Zonites:* Turchini & Broussy, 1935; *Spiraxis, Priodiscus*); or along the columellar muscle (*Labyrinthus:* Tillier, 1980); or along the lung roof (Endodontidae: Solem, 1976; *Oreohelix;* various Orthurethra: *Leptachatina, Cochlicopa, Chondrula, Ena, Imparietula, Klemmia,* etc.).

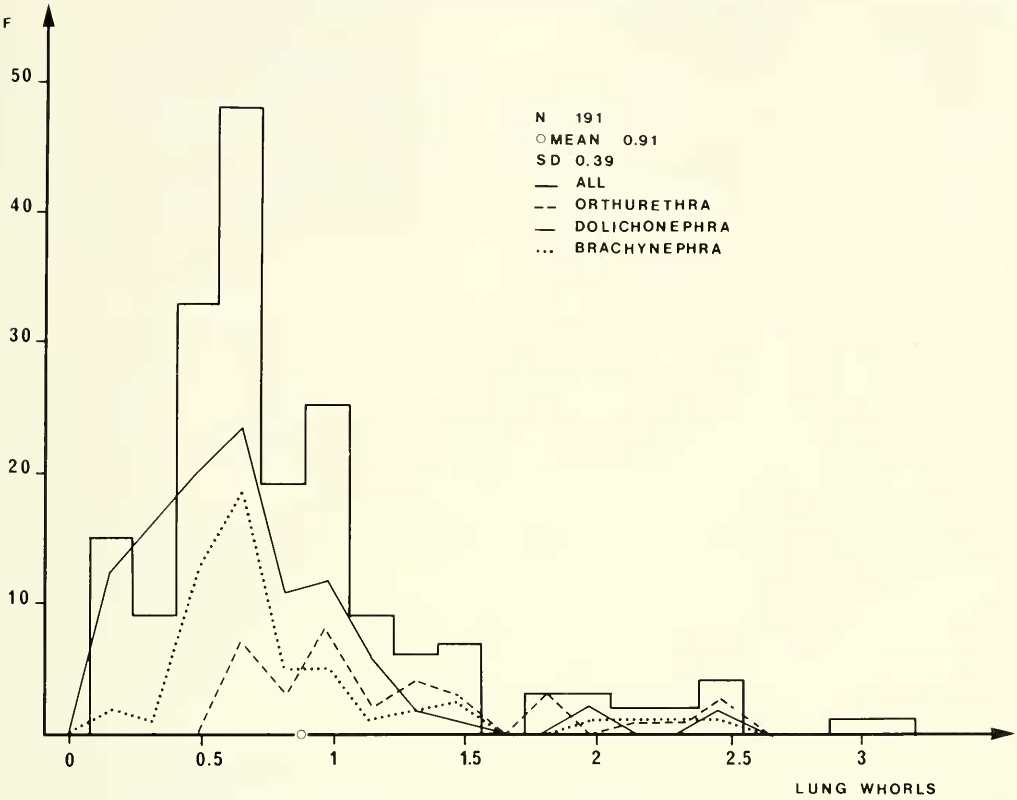
Respiratory mechanisms are wholly simple, although their physiology is imperfectly understood; whether inspiration is active or passive is still a matter of discussion (Ghiretti & Ghiretti-Magaldi, 1975). The lung cavity fills with air as the pneumostome opens and the diaphragm contracts to dilate the lung. After a while the pneumostome closes and the diaphragm relaxes, which produces a slight excess of pressure inside the lung cavity. Gaseous exchange occurs through the walls of the pulmonary venous system, and the cycle starts again. The lung cavity may also serve as a water reservoir (Blinn, 1964), a feature considered by Solem (1978) as essential for the success of land snails in colonizing terrestrial habitats.

The inner walls of the kidney sac form folds that resorb the wastes from the liquid coming from the pericardium *via* the reno-pericardial pore and canalize the residues to the renal pore and the ureter or ureteric zone. The morphology of these folds, or lamellae, has not been described previously and is here figured in the anatomical drawings. Their histology has been discussed by Bouillon (1960) and Delhaye and Bouillon (1972 b, c) in a few species. The inner wall of the kidney sac of the Stylommatophora might also have small caruncles, more frequent in the distal region of the kidney sac. In small animals, these caruncles seem equivalent to islets of lamellae (e.g. Figs. 246, 611), whereas caruncles are outgrowths on the surface of the lamellae in large species (e.g. Figs. 257, 691). I have no idea of the histology and function of such caruncles, and do not know whether the two types of caruncles are homologous.

The inner wall of the ureteric tube, when present, may also have folds. From their sample, Delhaye and Bouillon (1972b, c) concluded that these ureteric folds are present in the primary ureter of sigmurethran land snails only (i.e. in the portion of the ureter between the kidney pore and the top of the lung). I have shown that such folds occur also in the secondary ureter of sigmurethran snails and slugs (i.e. in the portion of the ureter between the top of the lung and the pneumostome; Tillier, 1983), and will argue further that the presence of ureteric folds is an effect of size.

We do not know how the system of cavities between the inner and outer walls of the kidney and ureter functions. I suppose from their arrangement that these lacunae allow the liquid resorbed from the kidney and ureter contents to flow back into the pulmonary venous system: the waste is probably more concentrated in the kidney-ureter system as it approaches the orifice opening into the lung cavity or pneumostome.

The presence or absence of lamellae or caruncles frequently allows us to recognize two or three anatomical regions in the kidney sac, from its proximal region (close to the



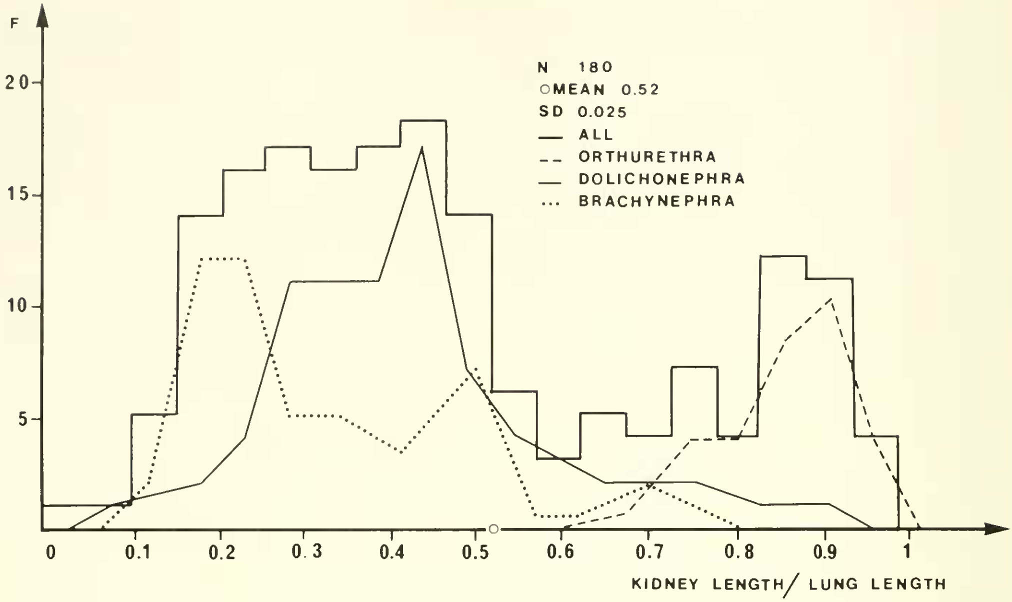
TEXT-FIG. 8. Length in whorls of lung in snails and semislugs studied (data, Appendix B).

reno-pericardial pore) to its distal extremity (usually close to the kidney pore). This morphological differentiation might correspond to a functional differentiation. In at least two orthurethran species (*Achatinella fulgens* and *Rachistia braunsi*), Delhaye and Bouillon (1972b) have recognized two histologically distinct regions that seemingly correspond largely to the morphological regions here recognized. In their interpretation, the proximal region is the kidney proper while the distal region functions as a ureter and will be called henceforth the ureteric region of the kidney.

Statistical analyses: External characters whose correlations with size and shape modalities (Appendix B) are studied are the degree of development of a ureteric tube, the relative length of the kidney and the lung length. The sample has been split into four or five classes of equal sizes for measurable data (limits of the classes, Appendix C).

The length of the lung used in the analyses is relative to the length of the visceral mass. LP being the length of the lung in whorls (Appendix B, Text-fig. 8) and LV the length of the visceral mass in whorls (Appendix B), the relative length of the lung is equal to LP/LV. It is strongly correlated with both LP and LV, and the result of the analysis is similar when LP is used.

The relative length of the kidney (LR) has been calculated as the ratio of kidney length to lung length, both being measured in mm from dissections of the pulmonary complex (Text-fig. 9). In general the points of reference for measurements are the viscero-rectal apex of the kidney (S1), the recto-pericardial apex of the kidney (S2) and the limit between lung and pneumostome roofs (S3). The relative length of the kidney is S1S2 / (S1S2 + S2S3). In heterurethran, transverse kidneys, S1 is the origin of the aorta because the lengthening of the visceral and rectal sides in such a kidney modifies the significance of measurements made with the viscero-rectal summit as a point of reference (Succineidae,



TEXT-FIG. 9. Relative length of kidney in snails and semislugs studied.

Ferussaciidae, some Oleacinidae). In U-shaped kidneys, S1S2 is the length of the pericardial arm of the kidney, measured from the apex of the U formed by the ureter (endodontoids, some discids). The relative length of the kidney has not been taken into account for semislugs and slugs whose kidney is longitudinal, but whose pneumostome is lateral (i.e. where the axis S1S2 diverges significantly from the axis S2S3).

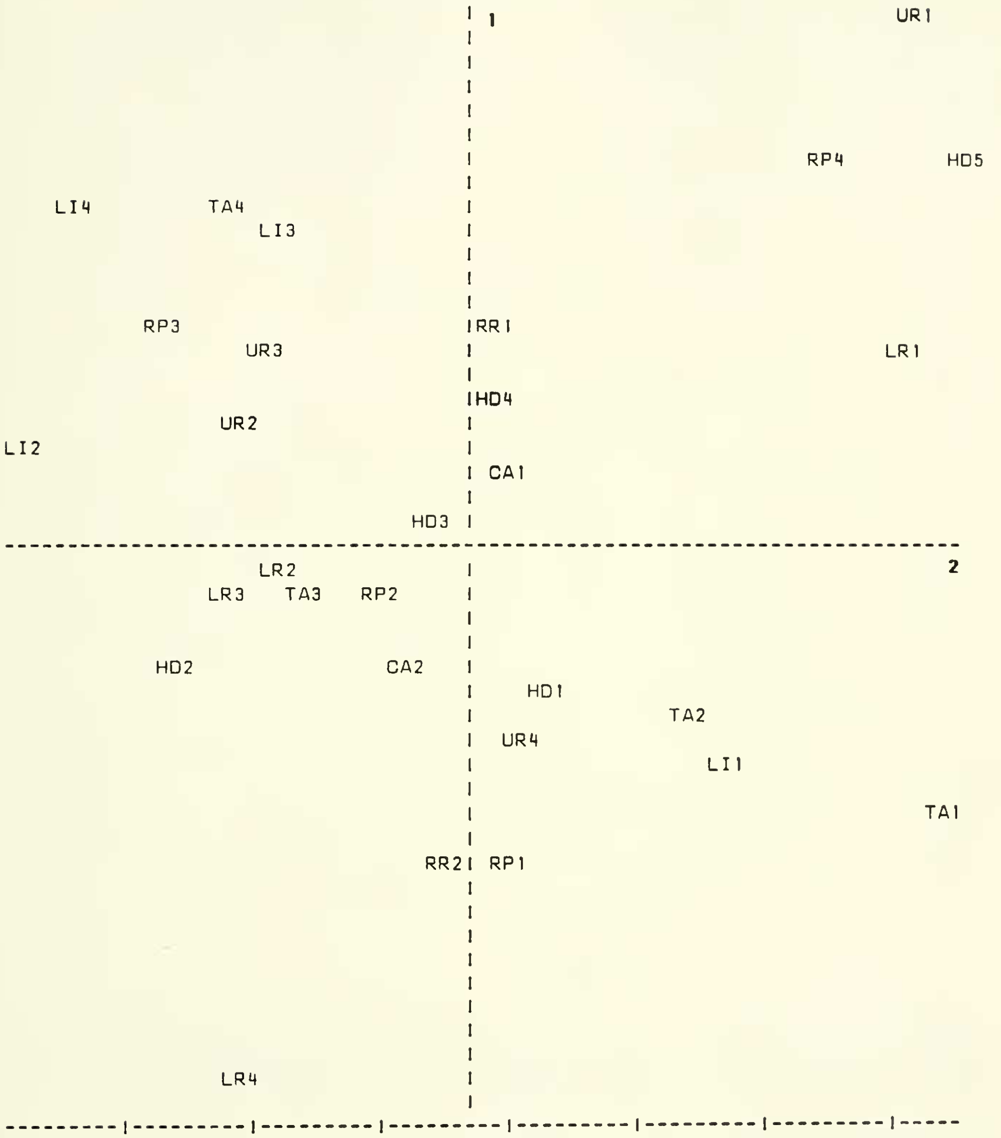
It is not necessary to insist on the importance of the length of the closed part of the ureter, which is a character of subordinal value in the Pilsbry-Baker system. Four degrees of closure of the ureter (Appendix E) have been distinguished: no closed retrograde ureter (UR1), which corresponds to orthurethran and mesurethran morphologies (mesurethran as originally defined by Baker in 1955; since then, snails with a partly closed ureter have been included in the Mesurethra because of general similarity); closed ureter reaching at most lung top (UR2); ureteric tube reaching a point between lung top and pneumostome (UR3); ureteric tube reaching the pneumostome (UR4 = full sigmurethry). Attempts to use classes of lesser amplitude showed rather weaker correlations than did such modalities, but this might be the effect of too small a sample size.

Numerous internal morphological characters of the kidney obviously occur in taxonomically restricted groups. Such characters, mentioned below, are not used in the general statistical analysis. The characters used are the number and density of the kidney lamellae and the density of their anastomoses, the internal division of the kidney into morphologically distinct regions, and the presence of caruncles.

Four modalities represent the morphological pattern of kidney lamellae (Ll): Ll1—few lamellae, not anastomose; Ll2— few lamellae, anastomose distally; Ll3—numerous lamellae with few anastomoses; Ll4—numerous lamellae with many anastomoses.

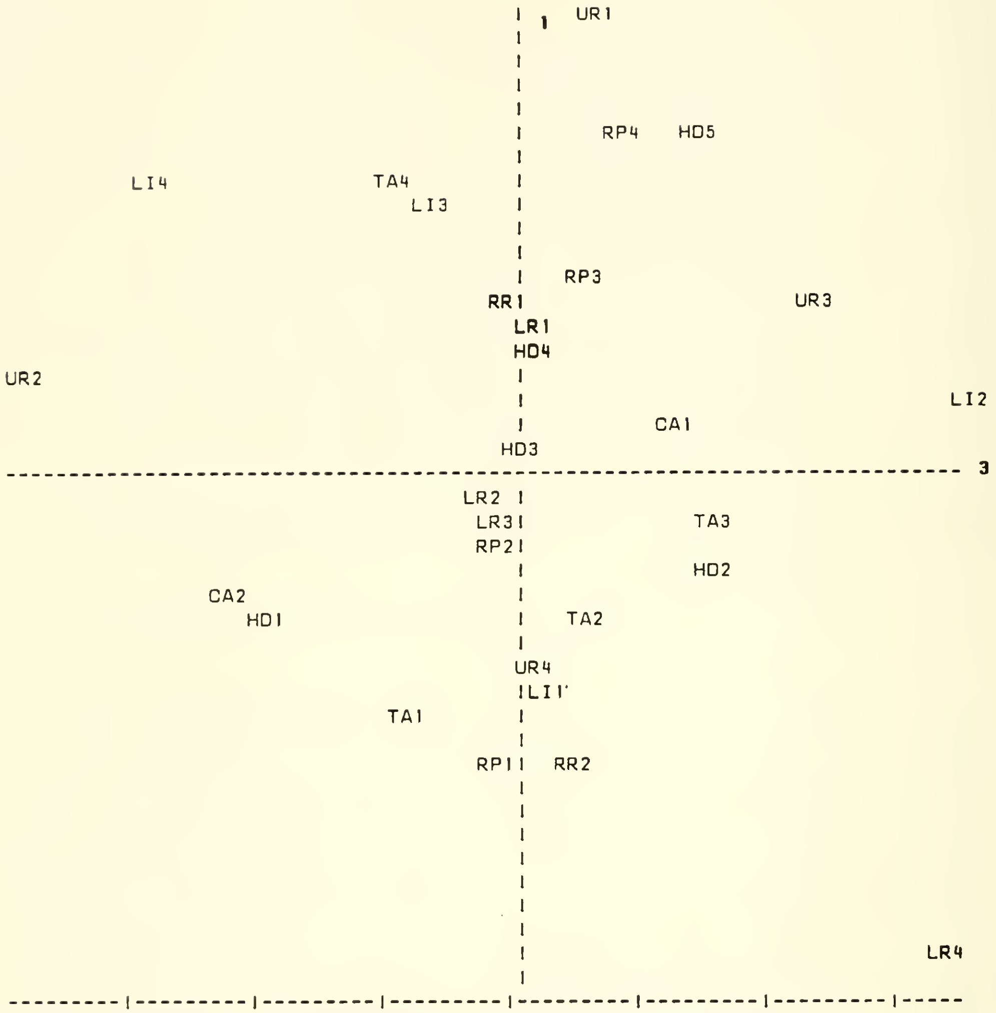
The morphological division of the kidney into several regions is represented by three modalities (RR): RR1—kidney homogeneous in internal morphology, with lamellae reaching the distal region and the level of the kidney pore; RR2—two distinct regions, the distal one usually lacking lamellae; RR3—three distinct regions, the median one either lacking lamellae or with lamellae different in appearance from those in the proximal region.

The presence and absence of caruncles have been respectively formalized as CA2 and CA1.



TEXT-FIG. 10. Factor map of correspondences among characters of pulmonary complex. Plane (1,2). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

The data set (156 species) has been analyzed in completely disjunctive form (each modality coded 0 or 1). Although not uninterpretable, the first analyses were very complex, involving a great number of axes. This complexity arose from the weight of the orthurethran snails that, being relatively numerous (31 of 156) and homogeneous in morphology, were discriminated by the first axes. This is why two analyses were performed: one taking only the non-orthurethran snails into account, the orthurethran snails being treated as supplementary lines; the second treating only the orthurethran snails. In the former (Text-figs. 10, 11, 12), the three first-axes represent only 31.3% of the total variance. This is why only correlations which are corroborated along other axes will be discussed; in some cases, correlations which appear only along the latter will be discussed,



TEXT-FIG. 11. Factor map of correspondences among characters of pulmonary complex. Plane (1,3). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

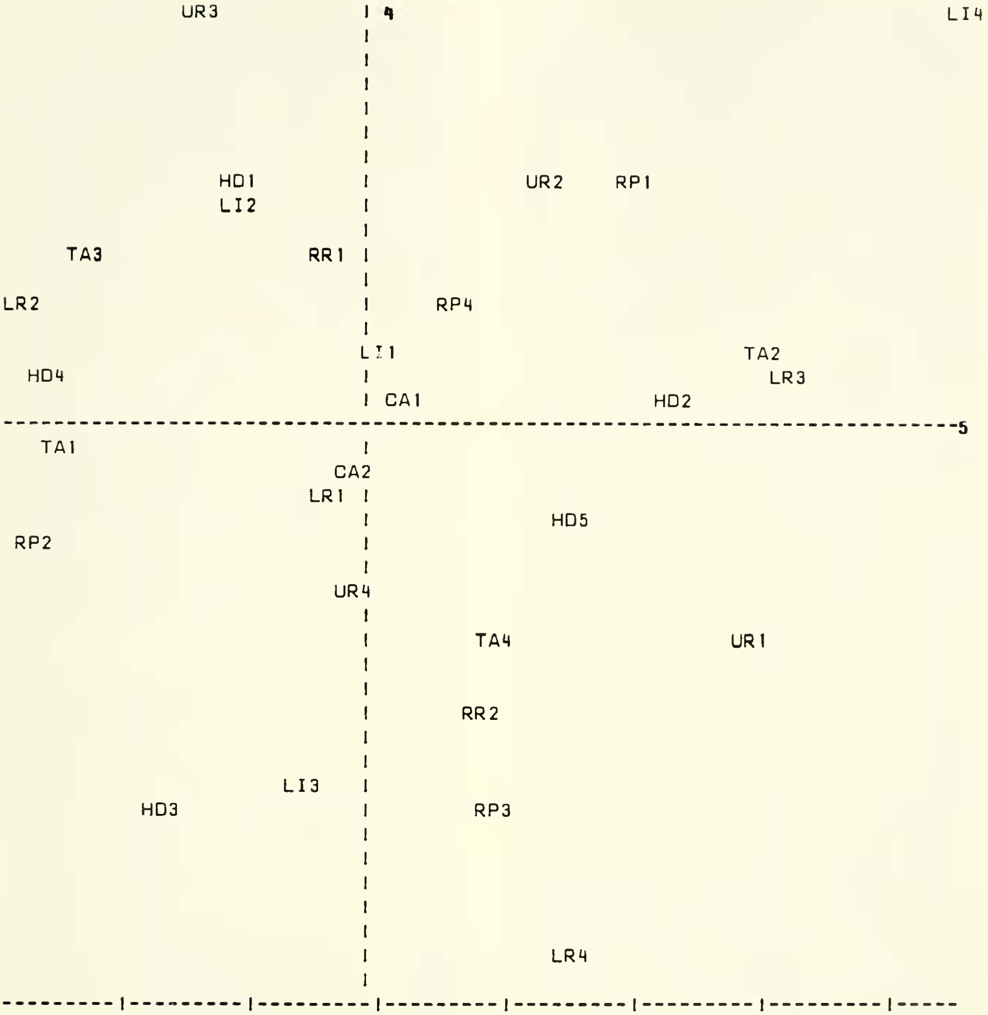
whenever their contribution is strong enough (Text-fig. 12).

Non-orthurethran pallial complexes

In this section lungs, when the kidney is either mesurethran or sigmurethran in the sense of Solem (1978), are discussed: the occurrence of partial sigmurethry in some of the Mesurethra *sensu* Solem (Acavidae, Figs. 406–469), and of mesurethry in some Sigmurethra *sensu* Solem (Corillidae, Figs. 470–491); Oreohelicidae, Fig. 493; Urocoptidae, Fig. 528) makes combined treatment necessary.

Factor maps: In summary, the plane (1,2) shows the relationships between extremes (Text-fig. 10), whereas the planes (1,3) (Text-fig. 11) and (4,5) (Text-fig. 12) show the relationships between mean modalities. The modality CA (caruncles) contributes to axis 3 only.

If one joins the modalities of every single variable in order in the plane (1,2) (Text-fig. 10), two directions appear: one, SE-NW, corresponds to size increase (TA1 to TA4); the other one, SW-NE, corresponds to kidney length decrease (LR4 to LR1). Axis 1 opposes complete mesurethry (UR1) to com



TEXT-FIG. 12. Factor map of correspondences among characters of pulmonary complex. Plane (3,4). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

plete sigmurethry (UR4); large size (TA4) to small size (TA1, TA2); short kidney (LR1) to long kidney (LR4); homogeneous kidney (RR1) to kidney with two internal regions (RR2); few renal lamellae (LI1) to numerous and anastomose lamellae (LI3, LI4). Axis 2 opposes large size (TA3, TA4) to small size (TA1, TA2); very short kidney (LR1) to all longer ones (LR2, LR3, LR4); few renal lamellae (LI1, LI2) to numerous renal lamellae (LI3, LI4); and mesurethran kidney (UR1) to any kidney having a portion of the ureter closed (UR2, UR3, UR4). The most important contributions to axis 3 are those of partly closed ureters (UR2 opposed to UR3), of flat shapes (HD1 opposed to HD2), of caruncles (CA1 opposed to CA2) and of few renal lamellae distally anastomose (LI2) (Text-fig. 11). Modalities whose contribution is stronger along axes 4 and 5 than along the first three axes are LR2, LR3, HD1, HD2, HD3, HD4, TA2, TA3, LI3, RP2 and RP3 (Text-fig. 12).

Discussion: With regard to degree of closure of the ureter, in the plane (1,2), LR1, RR1, RP4 and UR1 are opposed to LR4, RR2, RP1 and UR4 (Text-fig. 10). In other words, the absence of a ureteric tube is associated with a short kidney lacking internal differentiation, in a long lung. It is opposed to the presence of a ureteric tube closed as far as the pneumostome, which is asssociated with a short lung and often with the internal differentiation of the kidney into two distinct regions. These associations are totally independent of size, which varies in a direction normal to plane (1,2). Absence of a ureteric tube is also associated with elongate shapes (HD5), whereas all shapes are associated with not only complete, but also partial sigmurethry (UR4, Text-fig. 10; UR2 and UR3, axis 3, Text-fig. 11).

The correlation between elongate shape, short kidney and absence of a ureteric tube may have a functional cause. In very young snails, the lung is relatively shorter than in adults (growth allometry): to a first approximation, the lung is relatively longer when whorl number is increased. On the other hand, elongate shells have more whorls than flat shells (within the general correlation discussed above, correlation is better between large numbers of whorls and very elongate shape than within other groups of modalities in Text-fig. 5). If it is easier for land snails to develop a relatively long lung when shape is elongate (Text-fig. 5), then snails which functionally need a long lung because of the absence of a ureter, as discussed below, would frequently have an elongate shape.

The proposition that a ureteric tube is present whenever the lung is short appears as the corollary of Solem's remark (1978) that there are no slugs, i.e. no forms with reduced lungs, without complete sigmurethry. In all mesurethran lungs, a narrow zone, different in aspect from the lung roof, runs from the kidney pore along the rectal side of the kidney and along the rectum to the pneumostome; when sigmurethry is incomplete, such a zone prolongs the ureteric tube to the pneumostome. According to Van Mol (in Delhaye & Bouillon, 1972b), this zone is ciliated in the Clausiliidae as it probably is in all non-orthurethran lungs in which sigmurethry is not achieved (Schileyko, 1978b). It is often delimited along the kidney and rectum by one or two ridges, forming a ureteric groove. From its position, this ureteric zone or groove is homologous with a sigmurethran ureteric tube. If its function is to resorb water from the wastes, it is in first approximation half as efficient as a ureteric tube, length being equal, because its surface is about halved. Therefore, all other things being equal, such a groove should be twice longer than a ureteric tube, and this fact may explain why snails lacking a ureteric tube have a long lung.

Morphologies intermediate between full mesurethry and full sigmurethry are much more frequent than Wächtler (1934) thought, although the degree of variation is generally limited within each particular family. The families Corillidae and Urocoptidae, in which snails without a ureteric tube and fully sigmurethran snails occur, appear as two noticeable exceptions. The Clausiliidae and Cerionidae have no ureteric tube. In the Endodontidae, Oreohelicidae (+ Ammonitellidae), and Acavidae, of which some have no ureteric tube, the closed portion of the ureter does not run farther than the recto-visceral angle of the kidney. In the Bulimulidae (Odontostominae included), Rhytididae, Helminthoglyptidae, Helicidae and *Solaropsis,* the opening of the ureteric tube is between the top of the lung and the pneumostome, and often at the level of the latter. In all other non-orthurethran families, the ureter is closed as far as the pneumostome.

Delhaye and Bouillon (1972b) have insisted on the taxonomical importance of the presence of folds in the ureteric internal wall, observed by them only in the primary ureter of the Sigmurethra *sensu* Solem. Such folds may be found in the secondary ureter (Tillier, 1983). I did not note their presence during all dissections, and could not take them into account in factor analyses. However, I observed internal folds in the ureter of large Stylommatophora only, and it seems clear to me that the development of ureteric folds is related to large size: the ureter functioning as a water recouping system and its efficiency being proportional to its internal surface, any size increase requires a larger increase of the ureteric surface (area / volume). As lung length, and ureter length which depends on it, are not correlated with size, the necessary increase in ureter surface is obtained by the formation of folds. On the other hand, for a given size range, the frequency of the presence of ureteric folds is in proportion to the relative shortening of the lung and ureter.

However, ureteric folds are not the only compensatory structures developed in the process of shortening of sigmurethran lungs. In *Limax*, the primary ureter forms a flat pouch above the kidney (Simroth & Hoffman, 1908–1928); in the Parmacellidae and Athoracophoridae, the ureter ramifies into diverticulae interdigitating with the respiratory structures

(Tillier, 1984a); in *Succinea* (Succineidae, Fig. 224) and in various Limacidae, the ureter is prolonged by a caecum beyond the pneumostome along the lung roof border; in *Nata* and *Rhytida* (Rhytididae), the primary ureter describes one loop between the kidney and pericardium before running along the rectal side of the kidney (Fig. 382; Watson, 1934).

Such morphologies related to lung shortening aside, the arrangement of ureteric tubes is quite constant, except in some Helicellinae (Helicidae) in which a remarkable morphocline may be observed. In *Candidula* (Fig. 673), the ureter opens into a groove along the rectum, close to the top of the lung. The general arrangement is similar in *Leucochroa,* but here the ureteric tube is prolonged beyond the ureteric pore toward the pneumostome by a long caecum that runs between the rectum and the ureteric groove (Fig. 681); the wall between the rectum and this caecum is brownish and spongy (in alcohol). Finally, in *Helicella,* ureteric pore and ureteric groove seem absent: along the rectum the ureter seems to be reduced to a long, blind diverticulum. If there is really no ureteric pore, the wastes can be evacuated only through the anus, after they have been concentrated while passing through the spongy tissue between ureter and rectum. This arrangement is unique among pulmonates, and may be related to the capacity of *Leucochroa* and *Helicella* to live in xeric environments.

Like the development of ureteric folds, the density of renal folds and of their anastomoses is clearly related to size (Text-fig. 10) and illustrates the principle of similitude. The highest density of anastomoses (LI4) is also correlated with the presence of an incompletely closed ureter, reaching at most the recto-visceral angle of the kidney (Text-fig. 11). This morphological modality has been observed only in Malagasian, Ceylonese and Australian acavids, and its cause could be considered phylogenetic as well as functional (Figs. 416, 427, 466). Renal lamellae are generally more developed on the kidney roof (shell side) than on the kidney floor (lung side). However, in *Cecilioides* (Ferussaciidae) and in all American Oleacinidae, kidney lamellae have been observed only on the kidney floor (Figs. 358, 367). The same trend, although less developed, appears in snails here considered as Corillidae (*Sculptaria, Craterodiscus, Plectopylis;* Figs. 472, 480, 483).

It has been sometimes hypothesized that the absence of a ureteric tube should be compensated by the presence of an ureter within the kidney (Wächtler, 1934). Although there is doubtless a balance between the absence of a ureteric tube and the density of renal lamellae (Text-figs. 10, 11), I identified surely a differentiated internal ureter only in *Corilla humberti* (Fig. 489). In this species, the kidney pore opens in the middle of the rectal side of the kidney (Pilsbry, 1905). The kidney sac is divided into two regions by a transverse ridge. The distal region is itself divided into two regions by a longitudinal ridge, more developed than the other kidney lamellae, which isolates an internal duct running from the distal extremity of the kidney to the kidney pore. In two acavid genera lacking an ureteric tube, *Clavator* and *Strophocheilus,* renal lamellae are absent from a zone that runs parallel to the rectal side of the kidney and reaches the kidney pore (Figs. 446, 463). This zone might function as an internal ureter. However, in the Clausiliidae, *Macroceramus* (Urocoptidae) and other fully mesurethran snails, kidney lamellae converge on the kidney pore with a change in their orientation, but without any other morphological differentiation that could be interpreted as an internal ureter (Figs. 507, 515, 518, 526).

In factor analysis the presence of renal caruncles can be interpreted only along axis 3 (Text-fig. 11), where it is correlated with flat shapes (HD1). One possible interpretation, which is not very satisfying, is that the development of caruncles increases kidney surface, compensating for the relatively smaller size of the kidney when shape is flat; this decrease of absolute kidney size is correlated with decrease in lung length.

The internal differentiation of the kidney sac into two regions is strongly correlated with a fully closed ureter (UR4, Text-fig. 10). I can see no functional interpretation of this correlation, and the cause of this differentiation might be phylogenetic since a similar differentiation occurs in the Basommatophora and Orthurethra (Delhaye & Bouillon, 1972a, b; *v. infra*).

Lung length and kidney morphology are closely related, but the modalities of this relation also depend on other parameters in such a way that several types of kidney morphologies occur with each lung length. These other parameters are the presence or absence of a ureteric tube, and the taxonomic position. The kidney is always approximately triangular when associated with a long lung, and variations in absolute length of the lung are correlated with variations in length of the visceral mass (*v. supra*). We have seen (Text-fig. 10) that first, a relatively long lung is usually associated with a relatively short kidney and no ureteric tube; and second, a relatively short lung (RP1), even when disregarding slugs, is usually associated with a relatively long kidney (LR4), a fully closed ureter (UR4) and internal differentiation of the kidney sac into two regions (RR2). These correlations are independent of size and shape.

In snails having no ureteric tube, the kidney pore is never apical, but opens through the rectal wall of the kidney; in a few extreme cases it opens midway between lung top and kidney apex. The absence of any closure of the ureter is general only in the Clausiliidae and Cerionidae. In other families, some members of which have no ureteric tube at all (Acavidae, Corillidae, Urocoptidae), partly closed or fully sigmurethran ureters also occur. In true mesurethran snails, the lung has either a long absolute length (>1 whorl) in the Clausiliidae, Cerionidae and Urocoptidae, or a medium absolute length (about 0.7 to 1 whorl) but a long relative length (RP4, Text-fig. 10) in the Acavidae and Urocoptidae. As discussed above, the considerable length of the lung in mesurethran snails is probably a functional necessity.

In the family Urocoptidae, to which both mesurethran and sigmurethran snails belong, the shape of the kidney is nearly constant (Figs. 528, 532, 533). In the Acavidae, the ureter is never closed farther than the lung top, and the morphology of the pulmonary complex is often remarkable (Figs. 415–466): the kidney top (proximal end of the kidney) may be distal to the lung top, and the visceral wall of the kidney may be very oblique, nearly parallel to the suture, whereas it is usually subperpendicular to the latter. Correlatively the periaortic intestinal bend is distal to the lung and the kidney top, instead of proximal, and the first secondary pulmonary vein on the left is often much more developed than it is in any other family. Knowing that the visceral mass is shorter in most Acavidae than in other families including mesurethran snails (Corillidae excepted, Appendix B), I interpret this morphology to be related to shortening of the visceral mass: in snails having no ureteric tube or only a short portion of the ureter closed, the lung cannot be shortened below a limit that depends on the functional importance of the ureteric groove. Thus, as the length of the visceral mass decreases, the periaortic intestinal bend extends distally along the left side of the kidney. The pericardium and pericardial wall of the kidney are displaced distally because of the position of the aorta, but the recto-visercal summit of the kidney is less displaced distally; as a result the kidney tends to be elongate parallel to the suture, following an axis passing from its recto-visceral summit to the origin of the aorta. If deformation of the kidney is slight and if the last whorl has a large enough section, the kidney pore remains in approximately the same position (e.g. *Dorcasia*, Fig. 431); if deformation of the kidney is important and if the last whorl is narrow, the kidney pore appears displaced toward the recto-visceral summit of the kidney as in *Helicophanta* (Figs. 465, 466), sometimes as far as the level of the origin of the aorta, as in *Strophocheilus oblongus* (Hylton Scott, 1939) or in *Stylodon* (Fig. 450). In the case of *Stylodon*, the visceral mass might be secondarily lengthened because it is longer than in other acavids. The development of the proximal left secondary vein is probably related to change in shape of the lung roof, in which diminution of the proximal surface (between kidney and rectum) might be compensated by improving the irrigation of the distal surface. There is seemingly no strict correlation between this pattern of deformation and the partial closure of the ureter, but there is a partly closed ureter in *Pandofella*, which has the shortest lung seen in the acavids.

Like acavids, corillids have a relatively short visceral mass, but their lung is generally longer (0.8–1 whorl). Only in *Corilla* (Fig. 489; Pilsbry, 1905), which has a shorter lung than those of other observed corillids, are the kidney and lung top deformed in the same manner as in many acavids, although the first left secondary vein is not so developed as in some of the latter. All acavids are large snails, and *Corilla* is the largest of mesurethran corillids: adjusting lung surface and ureteric groove length to short length of the visceral mass is probably more critical in large snails. Perhaps the space for retracting the foot requires higher values of these parameters than is critical in relatively small snails, whereas the smaller area/volume ratio requires that lung surface and ureteric groove length be larger than is needed for foot retraction in large mesurethran snails.

In non-acavid Stylommatophora whose ureter is at least partly closed the length of the closed portion of the ureter increases as lung length decreases (Text-fig. 10), and there is no stylommatorphoran having a lung less than 0.5 whorl long whose ureter is not closed down as far as the pneumostome. Relative length of the kidney varies inversely with lung and visceral mass lengths (Text-figs. 10, 11, 12) because the absolute size of the kidney is nearly constant for a given body size, even in the first steps in limacization. Snails with an elongate shape associated with a short lung (Ferussaciidae, some Oleacinidae, Succineidae) are exceptional in having a very short kidney. In fact, the rectal and visceral sides of the kidney are much longer than the cardiac side in these snails, whose kidney appears transversally elongated (Figs. 224, 358, 361). This is the condition Pilsbry (1900a) called heterurethran, which justified for a long time the classification of the Succineidae in a separate suborder, although Watson had described heterurethry in ferussaciids as early as 1928. The arrangement of lamellae in heterurethran kidneys (Fig. 225) clearly shows that heterurethry is the result of elongation subperpendicular to the rectum on the visceral and rectal sides of a relatively short kidney. Because it is found only in relatively short lungs, heterurethry might be the result of lung shortening without shortening of the upper visceral mass in elongate snails having a short kidney.

The U-shaped kidney of some Charopidae, Punctidae and Discidae (Figs. 182, 186) somewhat reminds one of a heterurethran kidney. However, deformation in this case is due to the elongation of the rectal and visceral sides of the kidney along the rectum toward the pneumostome instead of perpendicular to the rectum; this is shown by the arrangement of the internal lamellae (Figs. 182, 183, 186). There is no simple, clear correlation between U-shape of the kidney and shortness of the lung. Charopid snails with a relatively short lung have a U-shaped kidney (*Paryphantopsis:* Solem, 1970; *Mystivagor*), but the kidney of endodontoid semislugs (*Ranfurlya, Otoconcha*) is not U-shaped.

Because kidney size can be modified only to a limited extent and limacization implies lung reduction, kidney morphology is necessarily modified in limacization. Modification in kidney morphology is probably necessary for preventing the kidney from occupying too much of the respiratory surface of the lung roof. Modifications in the lung proper were discussed elsewhere (development of the venation, formation of alveoli, development of air sacs: Tillier, 1983). In the first steps of limacization and in some more-advanced semislugs, the axis of the kidney, passing through the reno-pericardiac pore and the kidney pore, is directed toward the pneumostome, as it is in snails (e.g. Vitrinidae, Gymnarioninae, Figs. 325, 326). In further steps in limacization, there are three main patterns, morphologically and taxonomically well defined, in the modification of the kidney morphology related to limacization: compaction and rotation clockwise (in dorsal view), folding and rotation counterclockwise (in dorsal view) and formation of an annular kidney.

Kidney compaction is generally associated with rotation of the kidney axis clockwise in dorsal view, such that the kidney axis becomes approximately parallel to the longitudinal axis of the foot, while the pneumostome remains lateral. The kidney is shortened and thickened, and the density of kidney lamellae is increased. In the most advanced slugs (e.g. *Atoxon,* Fig. 336), the kidney is ovoid. Compaction occurs in zonitoid slugs (Daudebardiinae, Milacidae, Limacidae, ?Trigonochlamydidae), in Vitrinidae (*Plutonia*), in western helicarionids (Urocyclinae: Van Goethem, 1977), and in Rhytididae (*Schizoglossa*). As far as can be observed, the kidney is also compact in a similar way in the Athoracophoridae. In limacization of snails with a long head (and with an elongate shape? Oleacinidae: *Strebelia,* Testacellinae; Rhytididae: Chlamydephorinae), the pneumostome migrates backwards and the kidney is correspondingly rotated clockwise in dorsal view: the kidney axis remains approximately directed toward pneumostome (Testacellinae: Lacaze-Duthiers, 1887; Chlamydephorinae: Watson, 1915).

Kidney rotation and folding occur in Oriental helicarionids. Rotation is counterclockwise, and brings the kidney pore farther back than the pneumostome. The kidney axis tends to be perpendicular to the longitudinal axis of the foot. The kidney is not compact; on the contrary, and probably in order to avoid the kidney's covering the lung surface, its proximal part is first enlarged (Figs. 294, 297), and forms a flat lobe or lobes along the lung floor in further steps in limacization (Solem, 1966a). In these kidney lobes the arrangement of the kidney lamellae, converging toward the kidney pore, is not modified.

An annular kidney, surrounding the pericardium, occurs in the Arionidae (Philomycinae included). The structure of this extraordinary configuration is more easily understood and described in the North American semislug *Hemphillia* (Figs. 195–199) than in other arionids whose kidney is more compact in relation to more advanced limacization. In *Hemphillia* the renal ring does not entirely surround the pericardium, but is interrupted at the level of the origin of the aorta. Careful examination of the kidney in other arionids shows that the seemingly complete ring formed by the kidney around the pericardium results in fact from contact between the extremities of the horseshoe formed by the kidney sac: the annular kidney sac is interrupted by a wall below the origin of the aorta. Kidney lamellae converge toward the kidney pore, which is near the right side of the pericardium: one might suppose that the annular kidney is simply the result of flattening and expansion above and beneath the pericardium. The problem comes from the contiguity of the reno-pericardial and kidney pores (Fig. 198). This arrangement seems functionally aberrant, because the products of cardiac ultrafiltration should flow along the kidney sac surface before reaching the kidney pore; the usual arrangement, with reno-pericardial and kidney pores opposed at the two kidney extremities, seems much more efficient for this purpose than contiguity (however, in vaginulid archaeopulmonates, the reno-pericardial and kidney pores are also contiguous: Tillier, 1984b). This arrangement makes reconstruction of intermediate steps difficult, although not impossible.

The ureter of arionids starts at a point on the right side of the pericardium, at the level of the auricle (Figs. 197, 211). It first runs to the right towards the pneumostome; this section is internally smooth or ornamented with transverse folds of the inner wall (Figs. 197, 212). Then it turns back and to the left (*Hemphillia*, Figs. 197, 199) or backwards (slugs, Fig. 212) before turning again toward the pneumostome (Figs. 196, 199, 211). These two last sections are internally ornamented either with longitudinal folds and caruncles (*Hemphillia*, Fig. 199) or with longitudinal folds only (*Philomycus*, Figs. 211, 212). This internal morphology of the two distal sections of the ureter is unique among the Stylommatophora, and strikingly similar to the internal morphology of the kidney in endodontids, charopids and discids, whose internal renal morphology is characterized by the great development of two longitudinal folds and, frequently, caruncles (Figs. 169, 183, 186, 188). One possible hypothesis explaining this set of unique morphologies in kidney and ureter is that the distal part of the arionid ureter is homologous to a snail kidney, and that the arionid kidney sac results from secondary development of the reno-pericardial pore. The idea of the hypertrophy of the region of the kidney pore in slugs related to discids is not totally eccentric, for one abnormal specimen of the discid *Anguispira alternata* dissected had a hypertrophied kidney pore, internally ornamented with folds. This hypothesis would explain why the arionid ureter is similar in morphology to some snails' kidneys, and why the reno-pericardial and kidney pores are contiguous in the Arionidae. Unfortunately, comparative data on the ontogenetic development of the kidney that would allow the testing of this hypothesis are lacking.

Orthurethran pallial complexes

Contrary to what has been written, even recently (Boss, 1982), the kidney pore is not apical in orthurethran kidneys and does not open towards the pneumostome. It opens from the right side of the distal region of the kidney, and the frequent occurrence of a ridge delimitating a groove along the kidney toward lung top (e.g. Fig. 5) shows that wastes are evacuated from the kidney in this direction, as in all Stylommatophora. The mistake arises from the original description of the orthurethran morphology by Pilsbry himself (1900a), and may reflect the very poor quality of Pilsbry's microscope, emphasized by Baker (1958).

From the preceding paragraphs it is clear that orthurethran kidneys are not defined by the absence of a closed ureter as proposed by Pilsbry in 1900. Furthermore, Watson described a ureteric tube in *Acanthinula* as early as 1920; a similar structure was described by Solem in 1964 in *Amimopina* and it also occurs at least in *Rachistia* (Fig. 137). This tube does not extend farther than the recto-visceral summit of the kidney, but seemingly does not differ in any character from incompletely closed ureters found in some other Stylommatophora. Orthurethran pulmonary complexes are defined by great relative length of the kidney (80% to 99% of lung length, Text-fig. 9); by great absolute length of the lung (more than 0.7 whorls, Text-fig. 8, Appendix B); and by internal morphological differentiation of the kidney sac into two, often three distinct regions (e.g. Figs. 5, 6). The association of these three character states defines a group homogeneous for other morphological characters, i.e. the Orthurethra.

The results of partial factor analyses treating 31 orthurethran species are obscure. The only clear correlation is that of very small sizes to flat shapes, which may indicate an origin of most small orthurethrans by progenesis, for the very first whorls of most larger, elongate orthurethran snails are flatter than the adult shell. This confusion, contrasting with the relative clarity of the results for non-orthurethrans using the same modalities, shows how homogeneous the Orthurethra are in morphology. To obtain significant results, the sample should be larger to allow the use of modalities representing classes of lower amplitude. However, the results obtained here, as well as examination of the figures, admit of a few interpretations.

As in other snails, the increase in density of kidney lamellae and of their anastomoses is related to large size, and probably represents the same solution to the area/volume ratio problem. Kidney lamellae are few, not anastomose, and present only in the proximal region of the kidney (at the level of the pericardium) in small species, whereas they are numerous and reach the distal part of the kidney, where they anastomose, in large species (Figs. 5–142).

In species with either a ridge along the kidney and rectum (e.g. *Cerastua,* Fig. 134) or a ureteric tube along the kidney and a groove along the rectum (e.g. *Rachistia,* Fig. 137; *Acanthinula,* Fig. 87), the lung is shorter than in species without such structures which belong to the same groups: the lung is shorter in *Acanthinula* than in other valloniids, and in the Cerastuinae than in the Eninae and in the Chondrulinae among Enidae. It may be supposed that, as in other Stylommatophora, the formation of a ureter external to the kidney is related to lung shortening. The Cerastuinae show not only several steps in ureter formation, but also a strong and prominent pulmonary venation (Mordan, 1984) and particularly dense and anastomosed kidney lamellae. All these characters are related to lung shortening in other Stylommatophora, and there is no reason to suppose that it is not the case for the Cerastuinae. Therefore, they cannot be used individually to distinguish the Cerastuinae from other Enidae, as suggested by Mordan (1984): visceral mass shortening, including lung shortening, development of lung venation and formation of a ureteric groove and ureteric tube constitute a single synapomorphy of the Cerastuinae because the co-occurrence of these character states is a functional necessity.

The function of the distal region of the orthurethran kidney is ureteric (Delhaye & Bouillon, 1972b, c). It explains the great relative length of the kidney, its macroscopic internal differentiation and possibly the absence of limacization (reflecting the kidney sac would eliminate the ureteric zone along the kidney, and possibly the zone for storing wastes if such structures occur). A ureteric groove reaching the pneumostome occurred in only a few of the observed Orthurethra (*Orcula, Solatopupa, Chondrula, Imparietula, Cerastua, Rachistia, Amimopina*), whereas the kidney opening is always directed toward the top of the lung and a ureteric zone usually occurs along the kidney. Generally the ureteric zone seems to reach at most the recto-visceral summit of the kidney. The apparent absence of a ureteric zone along the rectum of most Orthurethra might result from poor observation, for most of them are small; but it is likely that, at least in large Orthurethra (e.g. Eninae), there is really no ureteric zone joining the top of the lung to the pneumostome. In the model proposed by Solem (1978), wastes are flushed from the lung cavity with pallial water; if this really occurs, presumably wastes are stored in the proximal region of the lung between flushes. This model implies a lack of water conservation by the snails, some of which live in dry environments. On the other hand, the presence of a zone of brownish tissue along the rectum of some enids, similar to that in *Helicella,* suggests that in some cases the wastes might be evacuated through the rectum and anus. Such a mechanism would prevent limacization, because in its course the rectum becomes separated from the right border of the lung roof.

Plesiomorphy and apomorphy in pulmonary complex

Plesiomorphy and apomorphy in the pulmonary complex of the Stylommatophora can be recognized by outgroup comparison with the pallial complex of the Basommatophora, Archaeopulmonates (Hubendick, 1978; Tillier, 1984b), plesiomorphic opisthobranchs (Gosliner, 1981) and prosobranchs (Fretter & Graham, 1962).

The occurrence of a lung ontogenetically distinct from the pallial cavity is a synapomorphy of pulmonates. The pulmonary complex of the Stylommatophora differs from that of most other pulmonates in two major characters: great absolute and relative length of the lung; and position of the kidney, which shares a wall with the visceral cavity, whereas in all other pulmonates, Otinidae (Archaeopulmonata) excepted, the lung roof surrounds the kidney. Because the lung is a neoformation, a lung extending around the kidney is apomorphic and the position of the kidney in the Otinidae and Stylommatophora is plesiomorphic. In the Archaeopulmonata and Basommatophora, the lung is never longer than about 0.5 whorl. In the Stylommatophora, such a short length is possible only if associated with a ureteric tube, which is apomorphic. Hence the long lung is a synapomorphy of the Stylommatophora, but is plesiomorphic within this group.

In all Archaeopulmonata and Basommatophora, the kidney is about 70% of lung length, i.e. shorter than in the Orthurethra. As mentioned above, the absence of a ureteric tube is plesiomorphic. The internal differentiation of the kidney sac into renal and ureteric regions is probably plesiomorphic, because this configuration occurs in the few archaeopulmonates and basommatophorans studied by Delhaye and Bouillon (1972a, c).

It may be concluded that the primitive arrangement of the stylommatophoran pulmonary complex should include: no ureteric tube; lung length more than 0.5 whorl, but as close to this length as possible; length of the kidney about 70% of lung length; probably a ureteric groove, because this structure is present in some orthurethrans and in all non-orthurethrans lacking a ureteric tube; kidney sac internally differentiated into two regions, supposedly renal and ureteric. No stylommatophoran snail examined has the whole set of character states; this implies that the morphologies observed do not represent a single morphocline (a primitive-like condition is approached in *Pagodulina* (Orculidae, Figs. 56, 57), but its lung length is too great to be plesiomorphic). However, it is essential to discuss morphoclines in which a short, otinid-like pulmonary complex is transformed into the various types of pulmonary complexes found in the Stylommatophora. The transformations proposed here entail two criteria, parsimony and homology in the distal region of the kidney, when differentiated. Both criteria may be contested: presence of an internal ureteric region, because there is no histo-physiological data showing that the differentiated distal region of non-orthurethran kidneys functions as a ureter; parsimony because we do not know whether evolution is parsimonious. Given these criteria, several patterns appear functionally acceptable. The first is the lengthening of the ureteric region of the kidney. This solution probably improves efficiency, but implies that the kidney occupies a larger portion of the lung roof and therefore reduces the respiratory area. This diminution may be counterbalanced either by lung lengthening or by a change in shape that increases the palatal and basal areas of the last whorl. Another solution, a change in vascularization, seems to occur only in relation to lung shortening. These are exactly the arrangements observed in the Orthurethra. The ureteric groove may have been lost in most of these snails, as discussed above. The second is dedifferentiation of the ureteric region of the kidney without closure of the ureteric zone. Such a modification allows kidney shortening and lung surface increase, but must be counterbalanced by lengthening of the ureteric zone of the lung roof, which itself is not possible without lung lengthening. Such a pattern occurs in the Clausiliidae, Cerionidae, Urocoptidae and Corillidae. If size is large and a ureteric tube is absent, a secondary internal ureter may be differentiated (*Corilla,* some Acavidae: *Clavator, Strophocheilus*). In such pulmonary complexes a ureteric tube may be secondarily formed, as in the Urocoptidae and Corillidae. A third pattern is the modification of the arrangement of the pulmonary complex. If the visceral mass becomes shorter before a sufficiently long ureteric tube forms, the pulmonary complex changes shape to preserve the length of the ureteric groove, as described above for the Acavidae.

The fourth is the formation of a ureteric tube before internal dedifferentiation of the kidney and kidney shortening: this solution allows change in shape and size without important change in the pulmonary complex arrangement, and is apparently the most successful in terms of radiation. A ureteric tube is associated with internal differentiation of a long kidney among all Aulacopoda *sensu* Solem, Achatinidae, Subulinidae, Systrophiidae, Haplotrematidae, Helminthoglyptidae, Helicidae, Camaenidae, Bradybaenidae, Sagdidae, Polygyridae and Ammonitellinae (Oreohelicidae). Formation of a ureteric tube might obviate lung lengthening: among all dissected genera belonging to these families, in only *Rumina, Sagda* and *Solaropsis* is the lung longer than one whorl (Text-fig. 8). If it is long enough or includes structures compensatory of low length (internal folds, caeca), a ureteric tube allows internal dedifferentiation of the kidney, which occurs in at least some genera of most of these families.

The fifth pattern is kidney shortening. This implies the formation of a ureteric tube; but dedifferentiation of the kidney, occuring after formation of a ureteric tube in a long kidney, might allow relative shortening of the kidney if the tube is long enough, and the resulting morphology is indistinguishable from that resulting from formation of a ureteric tube during the course of kidney shortening if no member of the family under consideration has either a kidney without any ureter, or a long kidney with a ureteric tube. This pattern occurs in the Rhytididae, Bulimulidae (including Odontostominae), Streptaxidae, Ferussaciidae, Oleacinidae and Succineidae. When lung shortening occurs, it is related to visceral mass shortening in the first three of these families, whereas it is associated with a peculiar shape in the three last ones, as discussed above.

These facts indicate convergence or parallel evolution (homoiology). It seems unlikely that closure of a ureteric tube, kidney shortening, and kidney internal dedifferentiation underwent reversal in polarity; but it has been shown above that high relative kidney length may result from shortening of a lung associated with a short kidney because the kidney tends to keep the same relative size, and therefore converge on the plesiomorphic condition. It is therefore extremely important to use the most plesiomorphic condition found in each family considered in discussing phylogenetic relationships of families. If the representatives of this condition are extinct or not studied, there is little hope of proposing relationships approximating real cladogenetic events.

In any case taxonomic use of the degree of closure of the ureteric tube may be meaningful only if related to other characters the functional value of which can be evaluated: on this point the criticisms aimed by Wächtler (1934) at the Pilsbry-Baker classification are just, although his scheme of morphoclines in the stylommatophoran pulmonary complex is much too simple. Criticisms made by Schileyko (1978a, b) are also proper only when taking this character alone into consideration: combination of this character with others, the evolutionary polarity of which can be determined, makes the construction of phylogenetic trees for the Stylommatophora both possible and justifiable.

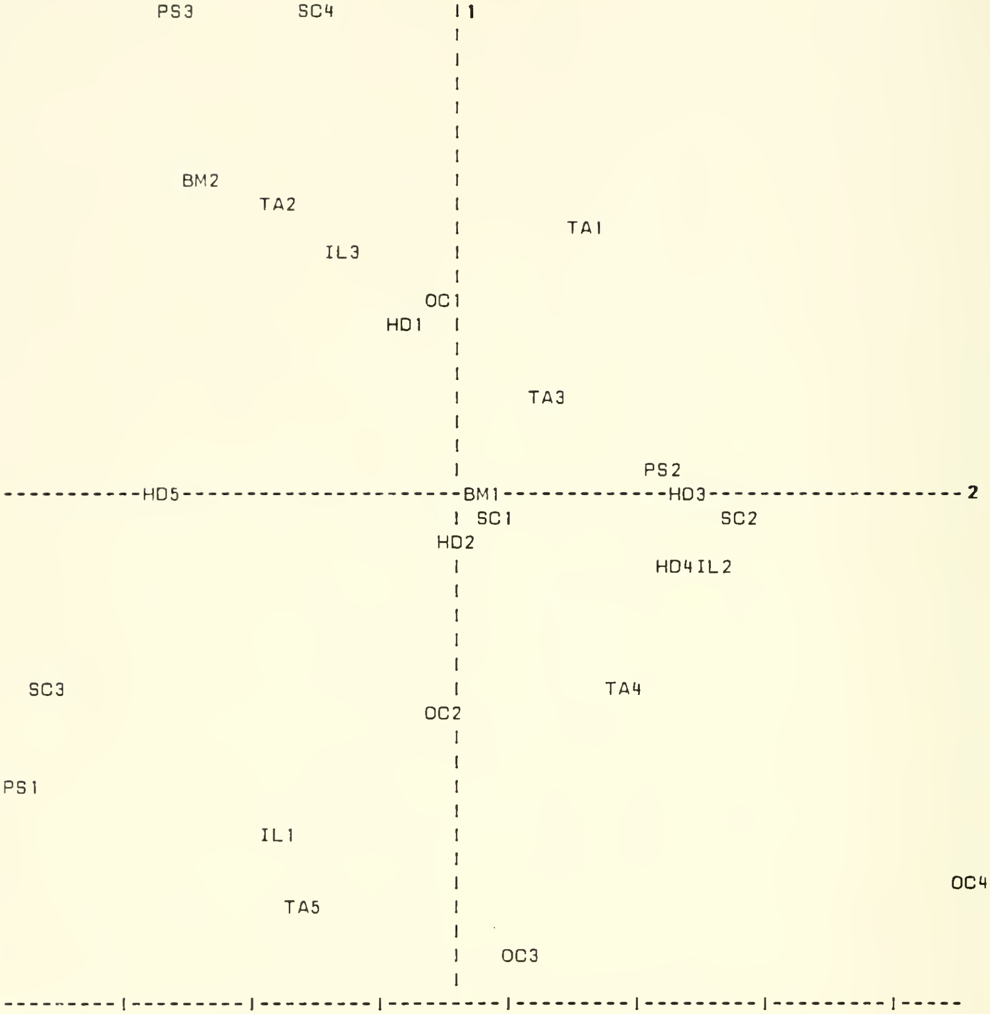
DIGESTIVE TRACT

The arrangement of the digestive tract in the Stylommatophora has been described above. I have emphasized and discussed elsewhere how the nearly complete absence of prior data leads to erroneous generalizations and conclusions (Tillier, 1984a); data and references on digestive tract anatomy in the Basommatophora and Archaeopulmonata may also be found elsewhere (Tillier, 1984b). The functioning of the digestive tract of pulmonates has been surveyed by Runham (1975).

In the factor analysis used in this chapter, the following variables and modalities have been used (Appendices B, C; Text-figs. 13, 14, 15):

1. Size: five classes with equal sizes (TA1 to TA5);
2. Shape: five classes with equal sizes (HD1 to HD5);
3. Buccal mass shape: spheroidal (BM1) or cylindrical (BM2); the latter shape corresponds to carnivory;
4. Oesophageal crop: absent (OC1); separated from gastric crop by a distinct portion of the oesophagus (OC2); separated from gastric crop by a simple constriction (OC3); as in OC3 but extending forward to the nerve ring (OC4);
5. Gastric crop: funnelform, widening from oesophagus to stomach (SC1); cylindrical (SC2); median portion inflated (SC3); funnelform, decreasing in diameter from oesophagus to stomach (SC4);
6. Gastric pouch: differentiated, separated from gastric crop by a constriction (PS1); differentiated, prolonging gastric crop without any constriction (PS2); reduced (PS3);
7. Intestine length: intestinal loops long, reaching proximally at least the level of the distal limit of gastric pouch (IL1); intestinal loops reaching a level between the distal limit of gastric pouch and the middle of gastric crop (IL2); intestine shorter, but intestinal loops distinct (IL3); intestinal loops reduced to an almost flat sigmoid (IL4).

In the factor maps (Text-figs. 13, 14, 15), large sizes (TA4, TA5) are opposed to small sizes (TA1, TA2) along the first axis: size is the principal factor of variation in the morphological characters of the digestive tract considered. Shapes load much less than do sizes



TEXT-FIG. 13. Factor map of correspondences among characters of digestive tract. Plane (1,2). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

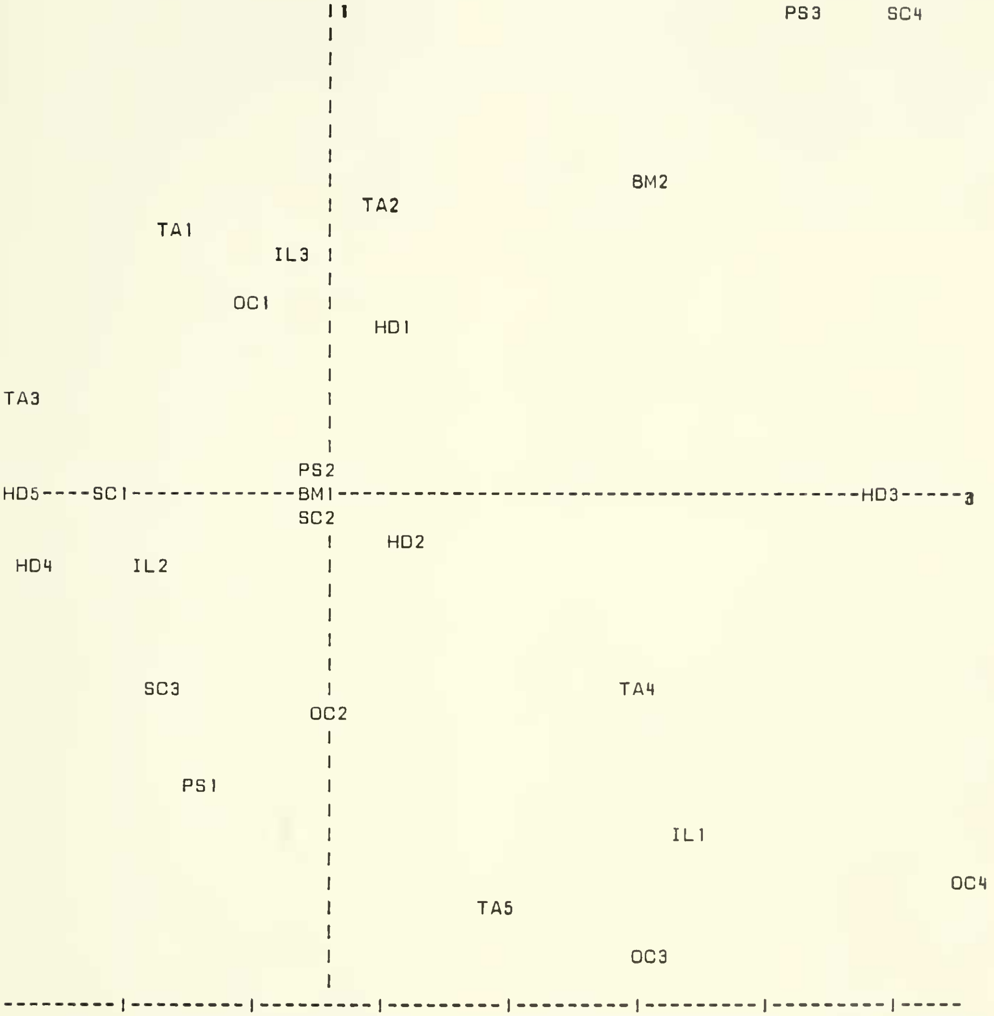
on the first axes: HD1 (flat shapes) contributes very weakly to axis 1; HD3, HD4 and HD5 contribute weakly to axis 2 but more strongly to axis 3; HD1, HD2 and HD5 contribute to axis 4 and HD3 contributes to axis 5. Overall correlations with size are principally in the planes (1,2) and (1,3) (Text-figs. 13, 14), and correlations with shape are in the plane (3,4) (Text-fig. 15).

Anterior digestive tract

The anterior digestive tract includes the buccal mass, salivary glands and oesophagus, part of which may be inflated to form an oesophageal crop.

Buccal mass, salivary glands: The buccal mass comprises a complex arrangement of muscles for protracting and retracting the radula and jaw. When the animal is not feeding, the radula forms a dorsally open tube covering the internal surface of the buccal cavity, and is posteriorly prolonged into the radular sheath, where teeth are formed. The jaw is above and forward of the buccal cavity. When the animal feeds, the radula is evaginated, and then invaginated as the jaw cuts the food, to bring the food back into the buccal cavity and oesophagus (Runham, 1975).

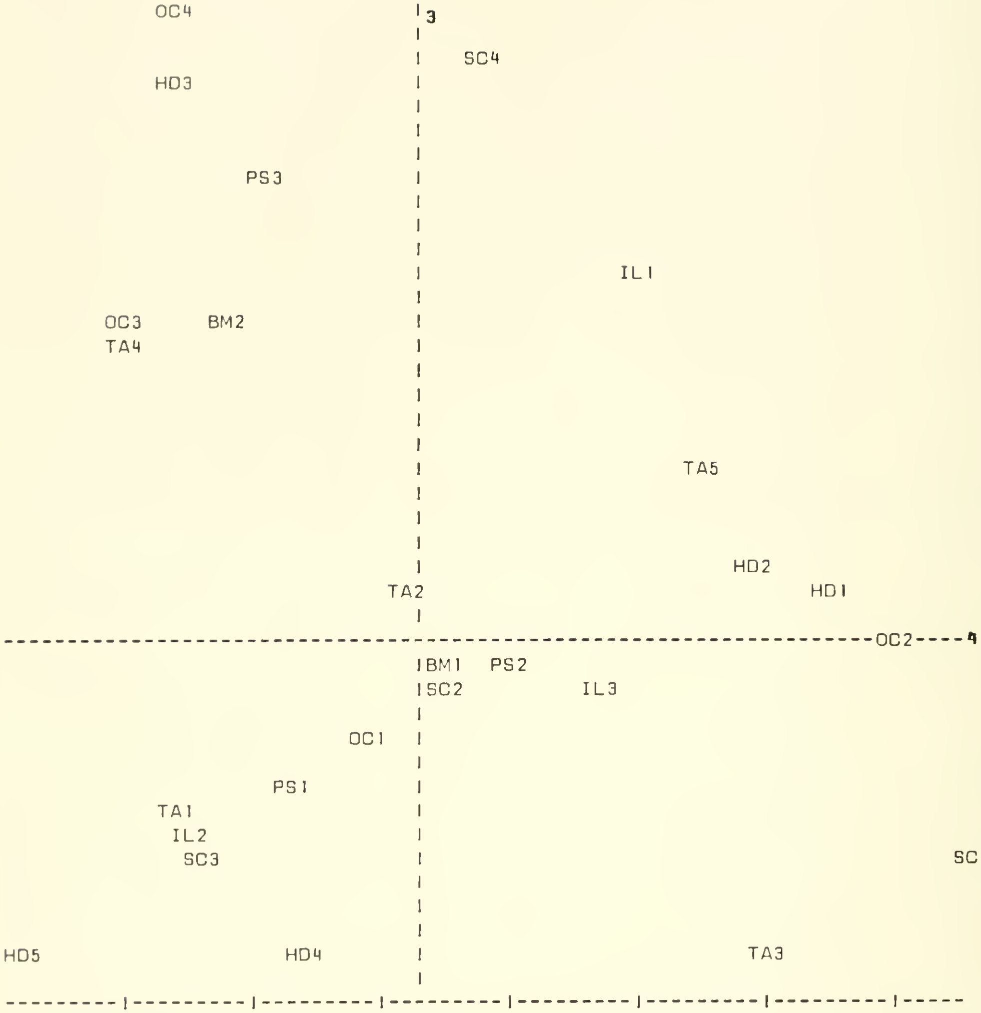
In carnivorous snails, radular teeth are dagger-shaped and the jaw might be reduced



TEXT-FIG. 14. Factor map of correspondences among characters of digestive tract. Plane (1,3). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

or absent. The buccal mass tends to be cylindrical and its outer surface has only transverse muscular fibers, instead of a complex arrangement of oblique muscular fibers. These modifications allow substitution for abrasion and cutting of vegetal matter by prehension, with subsequent shredding and swallowing of animal prey. Correlatively, the head is often longer than in non-carnivorous snails, the distal part of the genital apparatus is reduced in size and the genital orifice might be displaced backwards (in the Rhytididae), in order to increase space for housing the larger buccal mass (Watson, 1915, 1934). In some carnivorous snails, the buccal mass is so big that it cannot be contained in the pedal cavity and extends into the visceral cavity, under the diaphragm (Oleacinidae, Rhytididae, Streptaxidae; Figs. 371, 380, 397). In Text-figs. 13–15, modality BM2 indicates the position of the center of gravity of carnivorous species: carnivory is clearly correlated with well-defined morphological modalities of other parts of the digestive tract, whereas the contribution of BM1 is nil, indicating the association of this modality with all other character states of the digestive tract.

The position of the salivary glands along



TEXT-FIG. 15. Factor map of correspondences among characters of digestive tract. Plane (3,4). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

the oesophagus is variable among taxa, but I do not know the factors that determine this position. When an oesophageal crop is present, the salivary glands are appressed to each side of its anterior portion. Generally they are compact and made of numerous agglomerated small lobes. Their apparent size is relatively larger in some carnivorous Stylommatophora, on one hand (*Nata, Schizoglossa. Ptychotrema*; Figs. 381, 393, 394); and in large non-aulacopod species, on the other hand (e.g. Figs. 430, 630). In carnivorous stylommatophorans, the salivary glands are very thick and they seem to show a real increase in relative size. In large non-aulacopod species, the apparent increase in size of the salivary glands is rather a change in shape: the salivary glands are relatively thin, formed by relatively large flat lobes lying loose in a matrix of conjunctive tissue. The apparent fusion of the salivary glands around the oesophagus, formerly used in taxonomy (e.g. by Fischer, 1880–1887), is not, in my opinion, an important feature. If such fusion occurs, only the conjunctive matrix is involved and the duct of each lobe runs either to the left or right principal salivary duct.

Oesophagus, oesophageal crop: The internal surface of the oesophagus usually has a system of longitudinal ribs and grooves, more apparent when the animal is large and when the oesophageal wall is thick. The length of the oesophagus is variable, but this variation is probably related to variations in size of functionally more important organs rather than to a definite change in aptitude of the oesophagus proper.

Unlike oesophageal length, the development of an oesophageal crop, the internal ornamentation of which usually differs from that of the oesophagus *sensu stricto,* is probably functionally important. The oesophageal crop has been considered a general feature of the Stylommatophora (e.g. Franc, 1968). This is not true: about half of the species here examined do not have an oesophageal crop, and all intermediate stages between complete absence and occurrence of an oesophageal crop extending from the gastric crop to the nerve ring occur in the Stylommatophora.

Factor analysis shows a strong correlation between size and degree of development of an oesophageal crop (Text-figs. 13, 14). In general, small snails (TA1, TA2) lack an oesophageal crop (OC1); a small oesophageal crop (OC2) may be present in medium-sized snails (TA3) and is very frequent in large snails (TA4); very large snails (TA5) nearly always have a well-developed oesophageal crop (OC3, OC4). Among the latter, extension of the oesophageal crop forward to the nerve ring (OC4) is related to medium shapes (HD3, Text-fig. 15), in which the relative volume of the last whorl is more important than in other shapes. As discussed above, the proportions of the visceral mass are not related to size. The relationship between the degree of development of an oesophageal crop and size increase can be interpreted in terms of the principle of similitude, taking time into account (Lambert & Teissier, 1927): the development of a storage volume allows the increase in the time for digestion without increasing noticeably the time for feeding; correlatively the proportions in the visceral mass need not be altered.

Gastric region, intestine

The gastric region is composed of three parts: the gastric crop, which prolongs the oesophagus, from which it differs by its larger diameter and generally distinct internal ornamentation; the gastric pouch, which constitutes the proximal part of the digestive tract, and which is often separated by a constriction from the gastric crop; and the proximal intestine, which runs from the level of the orifices of the ducts of the digestive gland to the beginning of the periaortic intestinal loop. There is often a constriction between the proximal intestine and the distal intestine, by which the proximal intestinal loops and the distal rectum may be distinguished.

Gastric region: Commonly the differentiation in internal morphology of the gastric complex is relatively more important in large animals, and may allow the distinction between the various (functional?) regions.

All observed internal morphologies can be discussed in terms of a general plan of organization, in which two ventral ridges, delimiting a groove, would run from the upper end of the oesophagus into the openings of the ducts of the digestive gland, and from these openings into the proximal intestine, were the animals not torted. Because of the torsion and rotation of the visceral mass, these ridges, when present, run along the right side (underside) of the gastric crop, and along the left side (upper side) of the proximal intestine. The lower (left) ridge enters the anterior (left) duct of the digestive gland, from which a generally short typhlosole extends. The upper (right) ridge runs above the opening of the anterior duct of the digestive gland and enters the posterior (right) duct, from which a generally long typhlosole extends. The latter usually is not distinguishable farther than the constriction separating the proximal intestine from the beginning of the periaortic intestinal loop, when present. The groove between these two ridges is ciliated at least in the gastric crop (Rigby, 1963, 1965) and probably functions as a conveyor belt that carries food particles into and out of the digestive gland. The most frequent modifications of this general plan of organization are: absence of the portion of the right ridge between the two openings of the digestive gland; absence of the two crop ridges; and reduction or absence of the left typhlosole. Exceptionally the left typhlosole, issuing from the anterior duct of the digestive gland, is more developed than the right one, as in *Solaropsis* and *Labyrinthus* (Camaenidae?) (Figs. 556, 559).

Although unusual, the occurence of internal ornamentation on the dorsal side of the gastric crop is not exceptional. It is composed of longitudinal ridges, prolonging those in the oesophagus. In such cases, two more developed ridges delimiting the ventral groove are usually present, but this is not always the case and sometimes only the larger diameter of the gastric crop marks the end of the oesophagus.

When present, the internal ornamentation of the gastric pouch consists in ridges that prolong those in the gastric crop and disappear at the level of the entry into the proximal intestine. These ridges are generally more or less wrinkled and look different from those in the crop, especially when the latter is separated from the gastric pouch by a constriction. In a few acavids (*Stylodon, Acavus,* Figs. 447, 467) and in bulimulids *s.l.* with a well-differentiated gastric pouch (*Plagiodontes, Discoleus,* Figs. 537, 545), the gastric pouch is not regularly spheroid, but divided by a constriction in a plane tangent to both the gastric crop and the proximal intestine. Internally this constriction is marked by either a transverse ridge (*Stylodon*), or a change in the ornamentation of the stomach wall. A somewhat similar arrangement occurs in *Eua* (Partulidae), in which the part of the gastric pouch that prolongs the proximal intestine protrudes and is itself divided transversally by a ridge (Figs. 25, 26). In *Partula*, a similar protrusion of the lower half of the gastric pouch is less developed than in *Eua* and lacks any internal transverse ridge (Fig. 29). I do not know the function of such internal differentiations of the gastric pouch, which might be understood by observing the movements of the particles in it.

The typhlosoles are the only internal ornamentation of the proximal intestine, except in American oleacinids and in a few acavids in which the proximal intestine has longitudinal ridges (Figs. 365, 371, 372, 412, 430, 433, 440). Similar internal ridges occur at the level of the constriction between the proximal intestine and the periaortic intestinal loop, when present (*Ena,* Fig. 126; *Oxychilus,* Fig. 240).

The most common of the four shapes of the gastric crop here distinguished is the nearly cylindrical one (diameter nearly constant between the increase in diameter indicating the upper end of the oesophagus and the gastric pouch; SC2, Text-figs. 13–15; e.g. Fig. 280). It is not clearly associated with any body size or shape, and its corresponding modality, SC2, is located near the origin along the axes 1, 3, 4 and 5 (Text-figs. 14, 15). A funnelform gastric crop, regularly widening from oesophagus to gastric pouch, has been seen only in the family Discidae, including *Helicodiscus* (Figs. 184, 187, 190; SC1, Text-figs. 13–15).

The presence of an oesophageal crop inflated in its median portion (SC3) is correlated with strong differentiation of the gastric pouch (PS1), and with elongated shapes (Text-figs. 14, 15). The former of these correlations is obvious, for the posterior part of the gastric crop usually must become narrower when separated from the gastric pouch by a constriction. The correlation with elongate shapes of the visceral mass is more interesting, and probably indicates the usual pattern of change in the morphology of the gastric region as body shape changes from flat to elongate; this can be checked by examining variation in gastric region morphology in relation to shape variation in a group homogeneous in other anatomical characters, such as the Orthurethra (Figs. 1–146).

However, a few snails have a flat shape associated with an inflated gastric crop, as does *Zonitoides arboreus* (Gastrodontinae, Fig. 277) or *Vallonia albula* (Valloniidae, Fig. 84). The morphology of the gastric region of these snails forcibly reminds one of that in newly hatched snails (Ghose, 1963, and personal observations). Because flat snails having such a gastric morphology are very small, I interpret the apparent discordance between their gastric morphology and their shape as paedomorphosis resulting from progenesis.

The occurrence of a gastric crop of which the anterior portion is inflated (SC4) is correlated with the occurrence of an undifferentiated gastric pouch (PS3), small sizes (TA1, TA2), a short intestine (IL3, IL4) and the absence of an oesophageal crop (OC1). The correlation of this gastric crop shape with the absence of a differentiated gastric pouch is obvious: if, in any other gastric morphology, the diameter of the digestive tract decreases at the level of the gastric pouch, the anterior part of the gastric crop appears inflated (*v. infra*). Correlation with the absence of an oesophageal crop here might indicate identity of function of the two types of crops. From this interpretation it follows that, in the absence of dedifferentiation of the gastric pouch, a storage volume for food is acquired through increase in the volume of the anterior part of the gastric crop in small snails, and through differentiation of an oesophageal crop in big snails. The presence of such an arrangement is nearly the rule in the Aulacopoda group A *sensu* Solem (1978), and in endodontoid snails. However, the occurrence of this morphology in other taxonomic groups suggests that its interpretation should be more functional than phylogenetic (Orthurethra: *Auriculella,* Fig. 1; carnivorous families; Corillidae: *Sculptaria,* Fig. 470).

In American oleacinids (Figs. 364–374) and in *Priodiscus* (Rhytididae?, Fig. 375), the anterior part of the gastric crop extends to form a rostrum above the upper end of the oesophagus. Functionally, the formation of such a rostrum seems to correspond to the exaggeration of the trend in increase in volume of the anterior part of the gastric crop observed in all carnivorous snails. In such snails an oesophageal crop can hardly be developed without further anatomical modifications, because the space required for its development is occupied by the buccal mass.

The gastric crop is not distinct from the oesophagus in *Eua* (Partulidae, Fig. 26), and can be recognized only from internal morphological details in *Bocageia* (Subulinidae, Fig. 343). In both cases, this apparent regression in the development of the gastric crop is correlated (counterbalanced?) with the hypertrophy of the gastric pouch. This pouch exhibits a particularly important internal differentiation in *Eua* (Fig. 25).

In *Diplomphalus* (carnivorous, Rhytididae, Fig. 388), the digestive tract is a simple tube, in which there is hardly any internal or external morphological differentiation. This morphology might result from the association of carnivory (dedifferentiation of the stomach, *v. infra*) with whorls narrower than those in any other observed snails, and with specialization in diet, which consists at least in part of other snails' eggs (young and adult *Diplomphalus megei* were found in egg clutches of *Placostylus fibratus*).

The occurrence of a well-developed gastric pouch that prolongs the gastric crop without being separated from it by a constriction (PS2) is a general character of the Stylommatophora that occurs in all groups, associated with all shapes and sizes, although less common in large animals (Text-figs. 13, 14). The increase in the differentiation of the gastric pouch, indicated by the presence of a constriction between pouch and crop (PS1), is associated principally with large sizes (TA4, TA5, Text-figs. 13, 14), and secondarily with elongate shapes (HD3, HD4, HD5, Text-fig. 15). In the latter case, differentiation of the gastric pouch is associated with change in the shape of the gastric crop, as discussed above. Dedifferentiation of the gastric pouch (PS3) is associated with carnivory (BM2, Text-figs. 13–15), and (or) with small sizes (TA1, TA2). Because the gastric pouch is not differentiated in newly hatched snails, absence of differentiation of the gastric pouch might result from paedomorphosis through progenesis when associated with small sizes and few whorls.

The palatal surface of the gastric pouch has a fleshy appendix in *Eua* (Partulidae, Fig. 26) and in both *Euglandina* species I dissected (Oleacinidae, Fig. 371). The internal surface of the gastric pouch lacks any visible differentiation that might correspond to the development of this outer appendix in *Euglandina;* in *Eua* the wall of the stomach seems covered internally by a cuticle in the place to which the appendix is attached. I am unable to interpret the presence of such an appendix, which can hardly be considered homologous with cuticular and muscular plates in the stomach of other pulmonates (Hubendick, 1978) because of its arrangement.

In the Stylommatophora the shape of the proximal intestine varies from cylindrical to funnelform. This pattern of variation in shape is difficult to interpret. A funnelform proximal intestine is frequent in the family Zonitidae (Figs. 241, 248, 254), and in the family Oleacinidae (Fig. 371) in which the diameter of the proximal limit of the intestine approaches or equals the diameter of the opening of the gastric crop into the gastric pouch; but it occurs also in other families, e.g. the Discidae (Fig. 187) and the Acavidae (Fig. 440).

Intestinal loops, rectum: When present, the internal ornamentation of the intestine consists of longitudinal ridges and grooves having a radial symmetry. The principal typhlosole might sometimes extend into the periaortic loop, but I never observed it beyond the crossing of the intestine and the aorta. Although the intestine was not opened in all species dissected, the following general propositions seem reasonable: first, ridges and grooves are more frequent close to the anus than more proximally; second, they are also more frequent when the visceral mass is short; and third, they are particularly frequent among the Zonitoidea, whatever the degree of reduction of their visceral mass.

The internal intestinal ornamentation probably improves the absorption (of water?) through the intestinal surface by increasing this surface, and improves the efficiency of evacuating the feces. If this is true, occurrence of ornamentation allows the shortening of the intestine without major functional problems: such an advantage might explain in part the success of zonitoid slugs in their geographic area (Palearctic Parmacellidae, Limacidae, Milacidae, and Trigonochlamydidae).

With only one exception, and disregarding limacization, the intestine varies much more in length than in arrangement. Variations in relative intestinal length are approximately proportional to variations in size of the animals: increase in size requires a larger increase in intestinal surface (principle of similitude). The latter is most generally attained through increase in relative length of the intestine (IL1, IL2, TA3, TA4, TA5, Text-figs. 14, 15). The intestine of *Helicophanta* (Acavidae, Fig. 464) has one loop more than does any other stylommatophoran snail observed. This odd arrangement might be related to the conjunction of large size with visceral mass shortening. Very short intestines are associated with small sizes (principle of similitude, TA1, TA2) and with carnivory (BM2, Text-figs. 14 and 15). Most usually the intestine is nearly constant in diameter from its proximal end to the rectum, except in *Achatinella* and in zonitid snails, whose intestinal loops are wider than the other portions of the intestine (Figs. 16, 240, 241, 248).

In addition to the rectal wall, a second partition often separates the lumen of the rectum from the pulmonary cavity (Solem, 1966a). As far as could be observed, it seems that this arrangement results from the prolongation of the visceral cavity forward between the lung cavity and the rectum.

Limacization

The morphoclines and patterns of the digestive tract in the course of limacization have been described and discussed elsewhere (Tillier, 1984a). All the slugs here studied can be placed in one of these already described patterns. Three points should be borne in mind. First, in most cases and at least in its early stages, limacization involves dedifferentiation of the gastric pouch and development of a crop, the oesophageal or gastric origin of which can hardly be determined. Second, limacization also most usually involves at least in its early stages the shortening of the intestine; this shortening may be balanced by the development of intestinal caeca or of ducts of the digestive gland. Third, in advanced slugs, lengthening of the intestine may cause secondary coiling or hypertorsion of the digestive tract into patterns that are certainly not related to the torsion and coiling of the ancestral snails.

In view of the diversity of taxa showing limacization, the number of morphoclines in the patterns of the digestive tract in limacization is too low for their use in familial or suprafamilial classification. However, they might be useful within families to determine whether the patterns in two slugs whose close relationship is suspected are compatible, i.e. to determine whether two observed patterns might belong to a single morphocline. Compatibility of the digestive tract arrangements in a group of slugs and semislugs does not prove monophyly, but incompatibility obliges one to reconsider the monophyly of the group.

Discussion

The morphology of the digestive tract is generally more complex in non-stylommatophoran pulmonates than in the Stylommatophora, the family Otinidae excepted (Morton, 1955; Hubendick, 1978; Tillier, 1984b). Consequently, one might be tempted to suppose that the digestive tract of the Stylommatophora has been simplified in the course of evolution. However, the morphology of the digestive tract of the Stylommatophora is close to that of plesiomorphic opisthobranchs and of the Otinidae (morphology of the gastric pouch, contiguity of the openings of the ducts of the digestive gland: Gosliner, 1981; Tillier, 1984b). Consequently, using the Otinidae as an outgroup for digestive tract morphology, as is done for lung morphology, is more appropriate than using other pulmonate groups.

It then becomes clear that the most widespread character states are plesiomorphic. These are the spheroidal shape of the buccal mass (when diet is not carnivory), the cylindrical shape of the gastric crop, the differentiation of the gastric pouch without an anterior constriction separating it from the gastric crop. In plesiomorphic opisthobranchs and in *Otina* the intestine is relatively long (IL1 in the factor analysis). However, intestinal length is so often correlated with size in the Stylommatophora it seems likely that, if the primitive Stylommatophora were small, they had a relatively short intestine (IL3) that was secondarily either lengthened or shortened. From such an archetypal pattern five patterns emerge. First, increase of intestinal length, development of an oesophageal crop, and increased differentiation of the gastric pouch (constriction) are generally related to increase in size. Second, inflation of the median portion of the gastric crop associated with a gastric crop separated from the gastric pouch by a constriction is generally associated with elongate shape. Third, increase in the diameter of the anterior portion of the gastric crop associated with dedifferentiation of the gastric crop, lengthening of the buccal mass, and intestine shortening are generally related to carnivory. Fourth, a poorly differentiated gastric pouch, associated with a gastric crop having the median portion inflated, might result from paedomorphosis. Fifth, greater volume for food storage might be gained by the development of the anterior part of the gastric crop if size is small or if the animal is carnivorous, or by the development of an oesophageal crop (generally when size is increased).

The taxonomic distribution of the transformed character states implies parallel evolution, as is to be expected from the functional and statistical analysis presented above.

CENTRAL NERVOUS SYSTEM

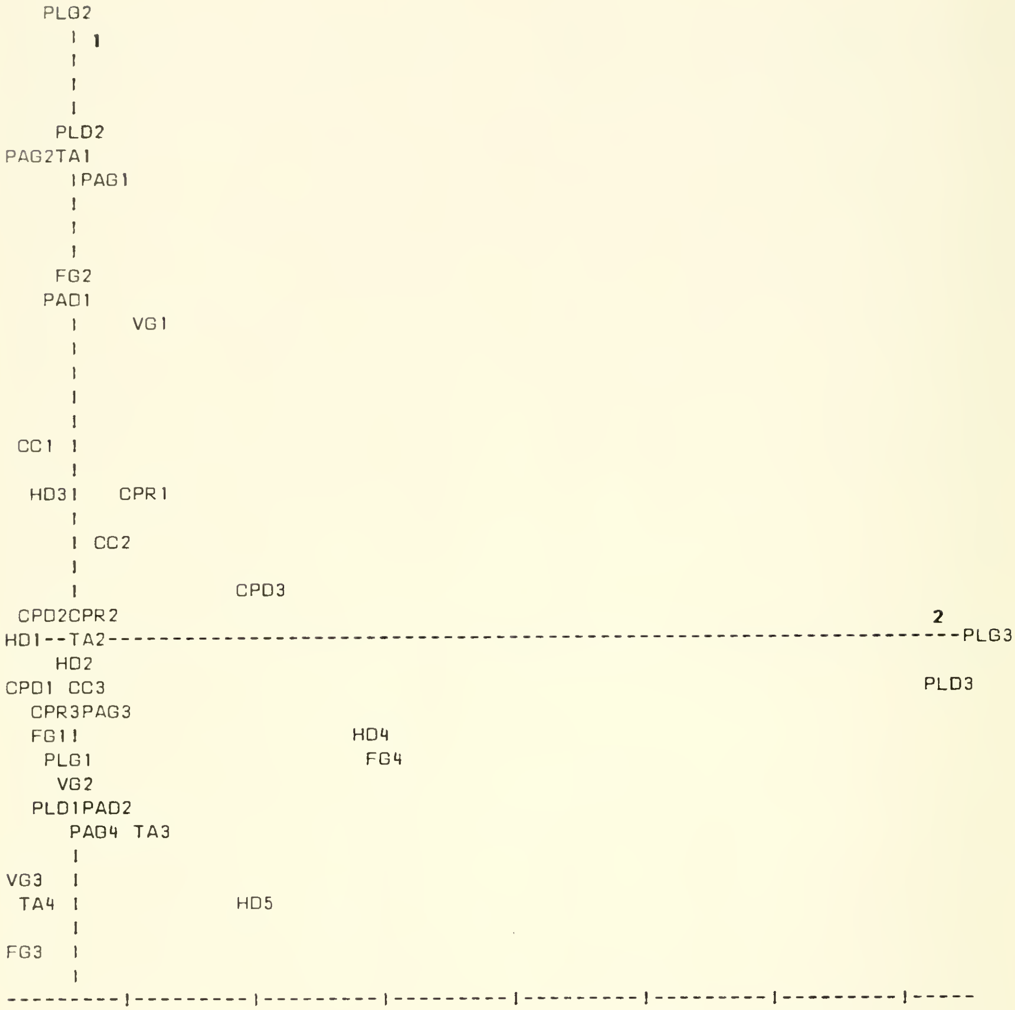
The general arrangement of the stylommatophoran central nervous system has been described above. The use of the variations in this arrangement for taxonomy and phylogenetic reconstruction has been attempted by Bargmann (1930) and Van Mol (1967). A precise nomenclature of the nerves issuing from the central nervous system may be found in the latter work.

Bargmann (1930) described principally the arrangement of the visceral chain, constituted by the visceral, parietal and pleural ganglia. She stressed the importance of the apparent fusion of the ganglia and recognized eight types of arrangements, seven of which occur in the Stylommatophora and can be grouped into four patterns: in the orthurethran type (Bargmann's type III), the visceral ganglion appears fused with the right parietal (as in Fig. 3); in the helicoid type (Bargmann's types I and V), the visceral ganglion appears fused with the left parietal (as in Fig. 698); in the other types the ganglia are either all distinct (Bargmann's types I, II) or fused with both sides of the visceral ganglion (Bargmann's types VI, VIII). The possibility of ordering these arrangements into morphoclines has been discussed by Bishop (1978).

Van Mol (1967) described principally the microscopic anatomy of the cerebral ganglia. With regard to phylogenetic patterns, he attributes the greatest importance to the degree to which the procerebrum is integrated with the metacerebrum (persistence of two procerebral commissures), and to the position of the origin of the peritentacular nerve (meso- or metacerebrum).

However, the taxonomic conclusions of both these remarkable works can hardly be accepted, mainly because of the small size of the samples examined: in both cases whole superfamilies are not represented, and observations in a single species are generalized to family level, or even to superfamily or suborder levels. A caricatural example is provided by Van Mol's use of the absence of a posterior procerebral commissure as a synapomorphy separating all Stylommatophora from the succineids, which justifies the suborder Heterurethra. In fact, Watson (1928) described a posterior procerebral commissure in ferussaciids; this single observation suffices to modify Van Mol's conclusions to a large extent. Bargmann's observations lack precision. On one hand, she seems not to have dissected the conjunctive sheath that envelops the ganglia and makes the discontinuities between them inconspicuous, particularly in relatively large animals (a few of Bargmann's dissections were seen by me in the BMNH). On the other hand, she seems not to have realized that the contact of two ganglia does not imply their fusion, even when no connective is visible: in general, two appressed ganglia are separated by a conjunctive wall (for example, compare the descriptions of the visceral chain in *Helix aspersa* by Bargmann and by Kerkut and Walker, 1975).

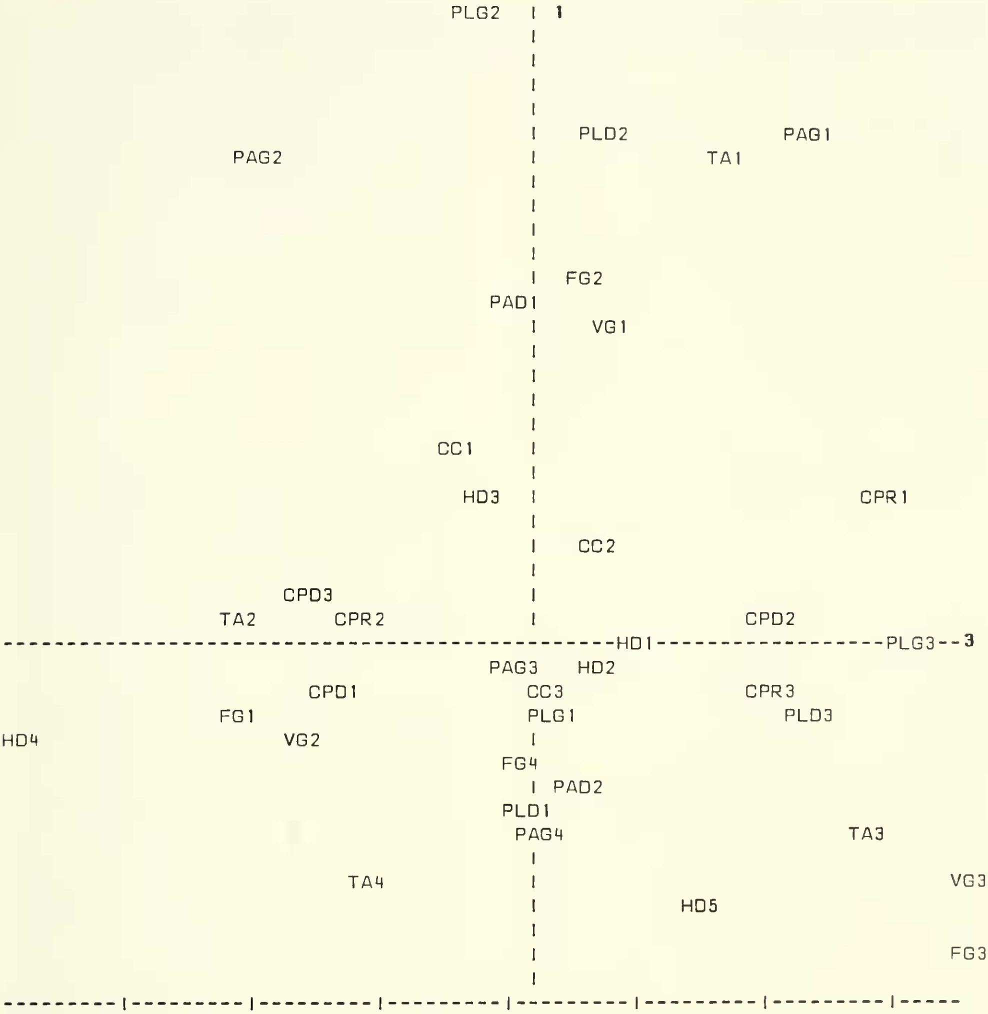
Having neither technical capacities nor time to examine microscopically the central nervous system of several hundred species, I did not use the microscopic characters shown and used by Van Mol (1967), i.e. the degree of integration of the procerebrum and the actual origin of the nerves. Similarly, I did not use the number and arrangement of the nerves originating from the central nervous system. Indeed, the conjunctive sheath around the central nervous system becomes opaque and hard when preserved in alcohol for a while, and nerve roots may easily be torn in dissection. This is why, although they have been figured, the number and arrange-



TEXT-FIG. 16. Factor map of correspondences among characters of nervous system. Plane (1,2). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

ment of the nerves depicted in the figures must be viewed with caution. Furthermore, it is likely that such characters vary at subfamilial levels, i.e. at a level lower than that considered here (see variations in the origin of the penial nerve as described by Baker, 1938, 1940, 1941).

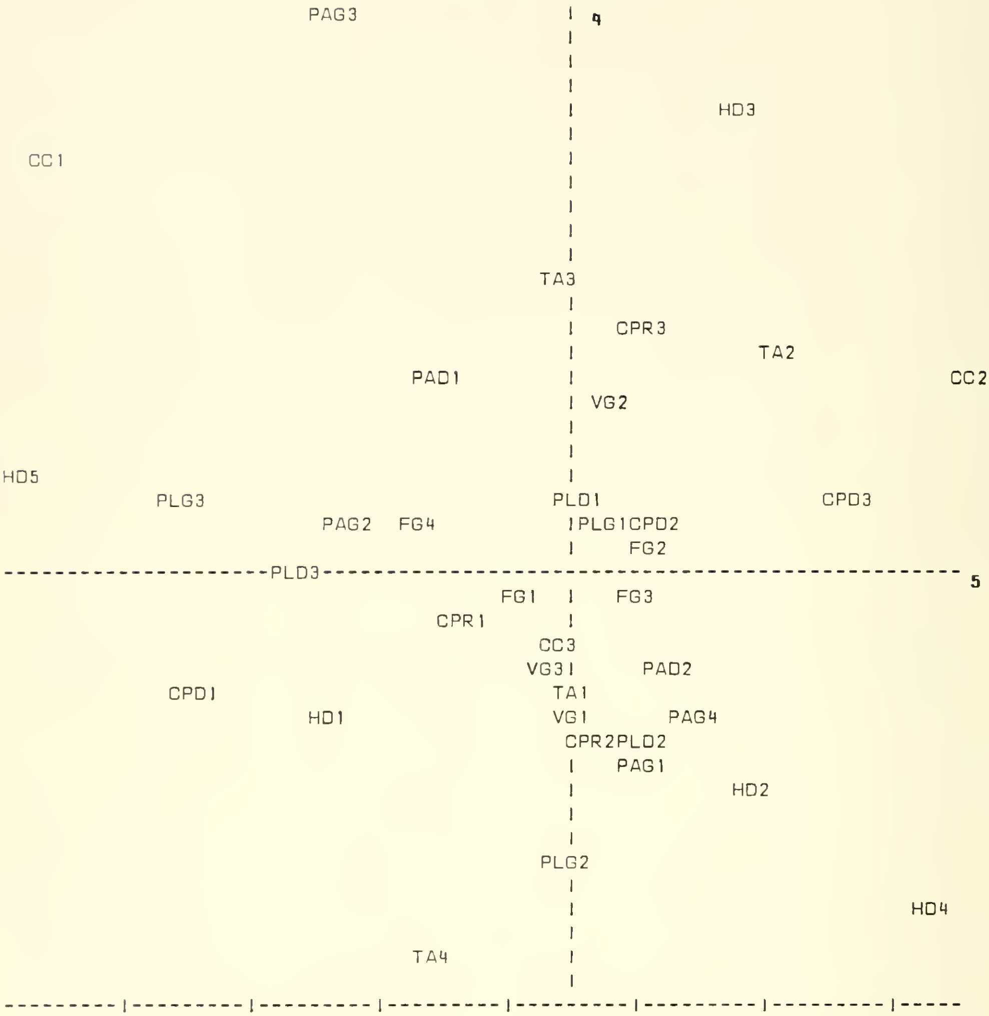
As a consequence the factor analysis here (Text-figs. 16, 17, 18) is limited to the arrangement of the ganglia in the central nervous system, in relation to size and shape. Semislugs and slugs are included. Four characters and 15 character states represent the arrangement of the anterior nerve ring, composed of the cerebral, pleural and pedal ganglia. The first character is the length of the cerebral commissure. The width of the right cerebral ganglion was measured from the origin of the optic nerve to the most posterior point, at which the cerebro-pedal connective joins the cerebral ganglion, giving three modalities: commissure distinctly shorter than cerebral ganglia width (CC3), about as long as the latter (CC2) or distinctly longer (CC3). The second is the length of the right cerebropedal connective. This length is an approximate index of the total length of the nerve ring without the visceral chain. Three modalities



TEXT-FIG. 17. Factor map of correspondences among characters of nervous system. Plane (1,3). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

were found: shorter than width of the right cerebral ganglion (CPD3), between one and two times right cerebral ganglion width (CPD2), more than twice longer than right cerebral ganglion width (CPD3). The third character is ratio between the lengths of the cerebropedal connectives (left/right). This ratio is an index of the asymmetry in the nerve ring, ventral chain excepted. There are three modalities: less than 0.9 (CPR1), between 0.9 and 1.2 (CPR2), from 1.2 to 2.5 (CPR3). The fourth is the position of the pleural ganglia on either side (PLG, the position of the left pleural ganglion; PLD, the position of the right one). The positions of the pleural ganglia are often not symmetrical, and the nerve ring may be nearly epiathroid on one side and hypoathroid on the other. Because the pleural ganglia form the extremities of the visceral chain, their positions also represent its relative position. Three modalities occur on each side: pleural ganglion closer to the pedal ganglion than to the cerebral ganglion (PLD1, PLG1), closer to the cerebral ganglion than to the pedal ganglion (PLD2, PLG2), very close to both the pedal and the cerebral ganglion (PLD3, PLG3).

Four characters and 13 character states



TEXT-FIG. 18. Factor map of correspondences among characters of nervous system. Plane (4,5). Data, Appendix B, Figs. 1–704; limits of classes, Appendix C.

represent the arrangement of the ventral chain. The first is the position of the visceral ganglion. Its modalities are: median plane of the visceral ganglion on the right side of the median plane of the pedal ganglia (VG1), median (VG2), on the left side of the median plane of the pedal ganglia (VG3). The second is the position of the right parietal ganglion; it has two modalities: in contact with the visceral ganglion only (PAD1), in contact with both the visceral and right pleural ganglia (PAD2). The third character is position of the left parietal ganglion. Its modalities are: closer to the left pleural ganglion than to the visceral ganglion (PAG1), closer to the visceral ganglion than to the left parietal ganglion (PAG2), in contact with the visceral ganglion only (PAG3), in contact with both the left pleural and visceral ganglia (PAG4). A compact visceral chain is represented by PAD2 and PAG4. The last is the apparent fusion of the visceral ganglion. The modalities are: none (FG1), with the right parietal ganglion (FG2), with the left parietal ganglion (FG3), with both parietal ganglia (FG4).

The size of the animals is represented by four modalities, *i.e.* four classes of equal size (TA1 to TA4). Their shape is represented by five modalities: for HD1, the H/D ratio is less than 0.6 (flat shells); for HD2, H/D is between 0.6 and 1.5 (helicoid shells); for HD3, H/D is more than 1.5 (elongate shells). HD4 represents semislugs and HD5 represents slugs.

In the factor maps (Text-figs. 16–18), the effect of variations in size appears along axis 1 (TA1 opposed to TA3 and TA4), axis 3 (TA2 opposed to TA3) and axis 4 (TA4 opposed to TA3 and TA2). The effect of variations in shape appears along axis 2 (HD4 and HD5, semislugs and slugs, opposed to snails) and in the plane (4,5) (HD1, HD2, HD3, shapes of snails).

Cerebral ganglia, cerebral commissure

The shape of the cerebral ganglia, which varies from clearly elongate to spheroidal, seems fairly constant within each family. Comparison of their degrees of elongation with Van Mol's data (1967) suggests that there is no direct relationship between shortening of the cerebral ganglia and the integration of the procerebrum with the metacerebrum.

The angle formed by the cerebral ganglia in a plane parallel to the pedal sole is variable. This angle seems to be generally larger when the visceral mass is shortened and the cerebral commissure is short, as shown by the figures: the longitudinal axis of the cerebral ganglia is generally subperpendicular to the cerebral commissure when the latter is long in snails with a long visceral mass; it is generally subparallel to the cerebral commissure in advanced slugs, and all intermediate arrangements occur in relation to cerebral commissure and visceral mass shortening.

Apparent shortening of the cerebral commissure is often due more to the expansion of the metacerebrum towards the median plane than to the actual shortening of the commissure proper. However, this is not so when the apparent difference in length is important, as when comparing, for example, the oleacinids (Figs. 362, 368, 373) with the clausiliids (Figs. 509, 511, 520). This case apart, correlations of the cerebral commissure length with other modalities appear along axis 1 (Text-figs. 16, 17), and particularly in the plane (4,5) (Text-fig. 18). Occurrence of a short cerebral commissure is partly related to large size (Text-fig. 16): no large snail has a long cerebral commissure, but some large slugs like *Parmacella* (Parmacellidae, Fig. 262) and *Oopelta* (Arionidae, Fig. 208) do. The converse is not true, for very small snails like *Varicella* (Oleacinidae, Fig. 368) have a very short cerebral commissure.

In snails a long cerebral commissure is usually associated with an elongate shell (CC1, CC2, HD3, axis 4, Text-fig. 18), and its shortening is associated with flat or globular shapes (CC2, HD1, HD2). This overall correlation, which often is not true in particular cases, might have a functional origin but might equally well be explained by phylogenetic relationships if both an elongate shape and a long cerebral commissure are plesiomorphic. At least in some corillids (Fig. 484) and in some oreohelicids (Ammonitellinae included) (Figs. 495, 498), a flat shape is associated with a long cerebral commissure, whereas a short cerebral commissure is often associated with an elongate shape in the Orthurethra, Urocoptidae (Figs. 530, 534) and Bulimulidae (Fig. 538).

Lateral connectives, pedal ganglia

As stated above, length of the cerebropedal connectives relative to cerebral ganglia width is an index of the total relative length of the nerve ring, the visceral chain excepted. On each side the length of the cerebro-pedal connective is slightly shorter than the sum of the cerebro-pleural connective length, pleural ganglion width and pleuro-pedal connective length. The lengths of the right and left cerebro-pedal connectives are subequal in about half of the observed species; in the other half the left cerebro-pedal connective is more commonly the shorter.

In the factor maps (Text-figs. 16–18), occurrence of a short right cerebro-pedal connective (CPD3) contributes mainly to axes 2 and 5; medium lengths (CPD2) contribute mainly to axis 3 and less to axis 2; long lengths (CPD1) contribute to axis 2 and more to axis 5. The ratio of the lengths of the left and right cerebro-pedal connectives (CPR1, CPR2, CPR3) contributes mainly to axes 3 and 4, but the contribution of the lowest values of this ratio (CPR1) to axis 3 is nil.

The shortest cerebro-pedal connectives are clearly related to limacization (CPD3, HD4, HD5; axis 2, Text-fig. 16). As might be expected, short length or apparent absence of the cerebro-pleural and pleuro-pedal connectives (PLG3, PLD3) is also related to limacization, which therefore is generally associated with shortening of the anterior nerve ring. Exceptions are one parmacellid (Fig. 261), and carnivorous slugs (*Plutonia*, Fig. 233; *Daudebardia*, Fig. 250; *Strebelia*, Fig. 374). In the case of carnivorous slugs, the retention of a long anterior nerve ring can be explained easily by the functional necessity for extending around the voluminous buccal mass associated with carnivory. On the contrary, medium and long cerebro-pedal connectives are clearly related to neither size nor shape, but long cerebro-pedal connectives are associated with a long cerebral commissure (CPD1, CC1; axis 5, Text-fig. 18). The latter association is probably the plesiomorphic condition of the anterior nerve ring, as will be discussed below.

Although varying less within families than between them, the ratio of cerebro-pedal connective lengths seems to vary independently of the other modalities to a large extent. However, relative shortening of the left cerebro-pedal connective is weakly correlated with flat shapes (CPR1, HD1; Text-figs. 17, 18); whereas its relative lengthening is slightly better correlated with elongate shapes (CPR3, HD3; Text-fig. 18). This pattern of variation can hardly be associated with hypertorsion in the visceral mass in relation to change in shape, which should cause the opposite effect. Variation in the asymmetry of the cerebro-pedal connectives might be related to variation in the angle between the longitudinal axes of the columella and the foot when the animals are active, but this hypothesis is purely intuitive and cannot be tested at present.

The cerebro-pedal and pleuro-pedal connectives insert on the posterior external surface of the pedal ganglia. The position of the pedal ganglia is related to connective length, the ganglia being farther back in the pedal cavity when the lateral connectives are short. In most cases, there are two commissures uniting the pedal ganglia. I do not know whether two commissures are present also when pedal ganglia are in close contact.

The pedal ganglia might be elongated parallel to the foot longitudinal axis (not seen in any large animal), subcircular, or elongated perpendicular to the foot longitudinal axis. The last shape seems to be related to shortening of the visceral mass, and no observed semislug or slug has pedal ganglia longitudinally elongate.

The statocysts are on the upper side of the pedal ganglia, behind the insertion of the cerebro-pedal connectives and usually on the inner side of the latter. In small snails with the pedal ganglia longitudinally elongate, the statocysts often form their posterior extremity. In large snails and slugs, especially when the pedal ganglia are transversally elongate, the statocysts are generally farther forward. In very large snails and slugs, they are generally deeply embedded in the pedal ganglia and are invisible without dissection.

Visceral chain

Position and length: The position of the visceral chain relative to the anterior nervous ring is determined by the ratio of the lengths of the cerebro-pleural and pleuro-pedal connectives on each side (PLG1, PLG2; PLD1, PLD2). As discussed above, extreme shortening of both connectives on each side (PLG3, PLD3) is usually related to limacization. In the factor maps (Text-figs. 16–18) these modalities contribute significantly to axis 1, and weakly to axis 4. Relatively important lengths of the visceral chain are represented by PAG1, PAG2 and PAD1, and short visceral chains by PAG4 and PAD2, which contribute mainly to axis 1.

A short visceral chain (PAG4, PAD2) is closely related to large size (TA3, TA4), whereas a long visceral chain (PAG1, PAG2, PAD1) is closely associated with small size (particularly TA1). This correlation is important for phylogenetic analysis, inasmuch as a long visceral chain is plesiomorphic: shortening of the visceral chain might have a different significance in small than in large animals, and cannot be used if not related to size. Like compaction of the anterior nerve ring, compaction of the visceral chain is also closely related to limacization (HD5); consequently close relationship of a slug having a very compact central nervous system with a snail having a very long central nervous system does not imply the former existence of a snail ancestor of the slug with a short central nervous system.

For a visceral chain of a given length, the diameter of the perioesophageal ring is smaller when the cerebro-pleural connectives are shorter than the pleuro-pedal connectives (PLG2, PLD2), than when the pleural ganglia are closer to the pedal ganglia (PLG1, PLD1). This explains why (Text-fig. 16) the occurrence of a short visceral chain is closely related to proximity of pleural and pedal ganglia (PAG4, PAD2, PLG1, PLD1, along axis 1): a short visceral chain is in general functionally impossible unless the pleural ganglia are close to the pedal ganglia, because it would strangle the oesophagus. Correlatively, the proximity of the pleural to the cerebral ganglia is unlikely unless the visceral chain is relatively long.

It can be seen in Text-fig. 16, along axis 1, that shortening of the cerebro-pedal connectives, when associated with shortening of the visceral chain, is not symmetrical. For a given length of the visceral chain, the pleural ganglion is closer to the cerebral ganglion on the right side than to that on the left (e.g. in some endodontoids, Figs. 147–183). This general asymmetry might be the direct result of gastropod torsion; it does not seem necessary to seek a further explanation.

Position of ganglia in visceral chain: In nearly all Stylommatophora, the right parietal ganglion closely touches the visceral ganglion. In contrast, the left parietal ganglion might be closer to the left pleural ganglion than to the visceral ganglion, closer to the visceral ganglion, or in close contact with the latter even in a long visceral chain. In very short visceral chains, the parietal ganglia touch the pleural ganglia.

The location of the visceral ganglion on the right side of the median plane is clearly related to a long visceral chain (VG1, Text-fig. 16). It is probably plesiomorphic, inasmuch as it might result directly from gastropod torsion. The displacement of the visceral ganglion toward the median plane and to the left side of the latter is related to shortening of the visceral chain, but only to the extent that limacization is not involved. This relation appears in the plane (1,2) of Text-fig. 16, where VG1 apparently is not associated with any shape modality, whereas VG3 (visceral ganglion on the left) is opposed to HD4 and HD5, which represent semislugs and slugs along axis 2. Whereas visceral chain shortening results in displacing the visceral ganglion to the left when related to size increase, it might be that shortening of the visceral chain related to limacization preserves to a large extent the arrangement of the ganglia in the ancestral snails. When related to visceral chain compaction associated with size increase, the displacement of the visceral ganglion to the left might be a simple mechanical consequence of the disappearance of the connectives, because the right parietal ganglion is generally larger than the left one.

Absence of fusion of the visceral ganglion with both parietal ganglia (FG1), or its apparent fusion with the right parietal ganglion (FG2), is correlated with small size and a relatively long visceral chain (Text-figs. 16, 17). Apparent fusion of the visceral ganglion with the left parietal ganglion is correlated with displacement of the former to the left, i.e. with shortening of the visceral chain in snails (VG3, FG3; axis 3, Text-fig. 17). Apparent fusion of the visceral ganglion with both parietal ganglia is strongly correlated with visceral chain compaction when associated with limacization (FG4, HD5; axis 2, Text-fig. 16).

The position of the left parietal ganglion closer to the left pleural ganglion than to the visceral ganglion (PAG1) might be plesiomorphic, because it occurs in the Otinidae and is probably plesiomorphic for all pulmonate groups (Tillier, 1984b). Its displacement toward the visceral ganglion seems independent of variations in the relative position of other ganglia, and therefore might be important for phylogenetic analysis (PAG2, Text-fig. 16). Unfortunately the distances between this ganglion and the visceral ganglion are comparable only if the visceral chain is not compact, and in this respect snails and slugs with a compact visceral chain provide no information; in other words, PAG2 seems correlated with a long visceral chain and small sizes (Text-fig. 16) only because large size is correlated with compaction of the visceral chain.

In carnivorous snails, the visceral chain is necessarily either relatively long or inserted close to the pedal ganglia, in order to encircle the large buccal mass. If lateral connectives are relatively short, lengthening of the visceral chain seems to have occurred, but the visceral connectives seem to have been unequally lengthened. Presumably only the connectives that were the longest before lengthening have been lengthened, which results in odd arrangements. The very originality of these arrangements makes them particularly interesting for phylogenetic reconstruction. In the families Rhytididae (Figs. 376, 385, 391) and Streptaxidae (Fig. 396) the visceral and parietal ganglia are compacted into a single mass that is united to the pleural ganglia by long connectives. These connectives are exceptionally long in the Streptaxidae (Fig. 396). In the family Systrophiidae (Fig. 401), only the left parieto-pleural connective is visible and is exceedingly long; the left pleural ganglion is appressed to the left cerebral ganglion, and the visceral and right parietal ganglia are seemingly fused together and appressed to the right cerebral ganglion.

Discussion

A polarity can easily be proposed for the morphoclines of most characters of the central nervous system, by outgroup comparison with plesiomorphic opisthobranchs and archaeopulmonates, in particular otinids (Gosliner, 1981; Hubendick, 1978; Tillier, 1984b). The following modalities are plesiomorphic: a long cerebral commissure; proximity of the left parietal and left pleural ganglia; probably rather long cerebro-pedal connectives; character states that might result directly from gastropod torsion, i.e. the position of the visceral ganglion on the right side of the median plane, a left pleuro-pedal connective shorter than the right one and a left cerebro-pedal connective shorter than the right one.

On the other hand, proximity of pleural and cerebral ganglia is probably apomorphic with respect to proximity of pleural and pedal ganglia. Comparison of the various patterns suggests that it results primarily from lengthening of the pleuro-pedal (and cerebro-pedal) connectives, followed by shortening of the cerebro-pleural connectives. The latter might disappear, to the extent that the visceral chain is long enough to allow retraction of the anterior digestive tract through the perioesophageal ring.

Proximity of the right parietal and visceral ganglia seems to be a synapomorphy of all Stylommatophora. Within the Stylommatophora, any long connective is apomorphic with respect to a shorter homologous connective, and the apparent fusion of two ganglia is apomorphic with respect to simple contact of the same ganglia, of which the limits remain distinct.

Although compaction in the central nervous system might be irreversible in most cases, the extreme length of some connectives, such as the lateral and visceral connectives of some carnivorous snails (Streptaxidae, Systrophiidae), can hardly be plesiomorphic. It seems that some connectives might lengthen in the course of evolution insofar as they are not very short, but the secondary development of a connective between two appressed ganglia is unlikely.

CHARACTERS OF STYLOMMATOPHORAN FAMILIES

In this section, before discussion of phylogenetic patterns in the Stylommatophora, an account of temporal and geographical distribution, and of the amplitude of the variations seen, is given for each family. Transfers at infrafamilial levels are tentatively justified. The order of presentation of the families presupposes the next section, a better approach than following here an order that will be rejected a few pages further. In the course of this systematic description, some groupings and transfers are discussed and justified. The most plesiomorphic character states seen in each family are summarized, in order to allow the phylogenetic reconstructions attempted below: the data are too numerous to be easily handled for building phylogenetic trees, and the most reasonable way to reduce their number seems to be to use only the most plesiomorphic states in each group for which monophyly is accepted. This approach, of course, implies that the direction of evolutionary change was correctly stated and that reversal can be neglected at familial and suprafamilial levels. This operation is equivalent to replacing members of a family by their hypothetical closest common ancestor (CCA).

In the course of the discussion, the results of the preceding sections are used, in part as a table of character states ordered from 1 (= plesiomorphic) to n (= apomorphic), together with two phenetic classifications, one for the species dissected and one for the families (Appendix E, Text-figs. 19, 20). These phenetic classifications are not at all definitive, but provide indications of similarity among taxa that can be used in further discussions.

Both phenetic classifications are ascending hierarchical classifications (Jambu & Lebeaux, 1979), built by the CAHCAR program in the ADDAD package (CIRCE) from the data of Appendices B, C. The limits of the classes, which are not the same as in the preceding partial factor analyses, are given in Appendix D. All the data were recoded 0 or 1, but no other change was made; missing data were coded 0. The data table for families was obtained by summing the lines representing the members of each family column by column, and recoding.

The conclusions of the preceding discussions have been used to determine the value of each character state in the table of ordered character states (Appendix E). The limits for each character state are the same as in Appendix D and as in the phenetic classifications; only the coding is different. Characters for which no direction of evolutionary change can be proposed have been eliminated.

When two paths are possible from a single plesiomorphic state, one has been noted 1, 2, 3, 4, etc. and the other 1, 2′, 3′, 4′, etc. For further analyses such data were recoded in two columns, as explained below.

Orthurethra

In nearly all the Orthurethra, the kidney is very long (LR2′), internally divided into at least two morphologically distinct regions (RR1), and without a ureteric tube (UR1). The few exceptions will be mentioned in the descriptions of the families to which they belong. No orthurethran is carnivorous (BM1). The oesophageal crop is most usually absent (OC1), sometimes little developed (OC2). The gastric crop is cylindrical (SC1) or inflated in its median portion (SC2). The gastric pouch is always differentiated (PS1, PS2). The intestine is generally rather long (IL1). Contrary to Bargmann's opinion (1930), the visceral ganglion is not always seemingly fused with the right parietal ganglion (FG2). The right cerebro-pedal connective is usually shorter than the left one. The lateral connectives are always distinct (PLG and PLD 1 and 2).

Far more precise descriptions than those presented here, but dealing with fewer taxa, may be found in the remarkable work of Steenberg (1925).

Achatinellidae (+ Tornatellinidae) (Figs. 1–24): The grouping of the families Achatinellidae and Tornatellinidae has been proposed by Cooke and Kondo (1960). Although not discussed by them, this grouping clearly seems based upon overall similarity and geographical distribution. Although I do not know of a synapomorphy of the two groups, uniting them in a single family seems justified from the data presented here on three grounds. First, all characters retained (Appendix E) either have the same state in both groups, or are more apomorphic in *Achatinella* than in non-Achatinellinae achatinellids; second, in the phenetic classification of the species, the three species the closest to *Achatinella* are tornatellinids (Text.-fig. 19); and third, in the phenetic classification of the families, the two groups are more similar to each other than to any other family (Text-fig. 20).

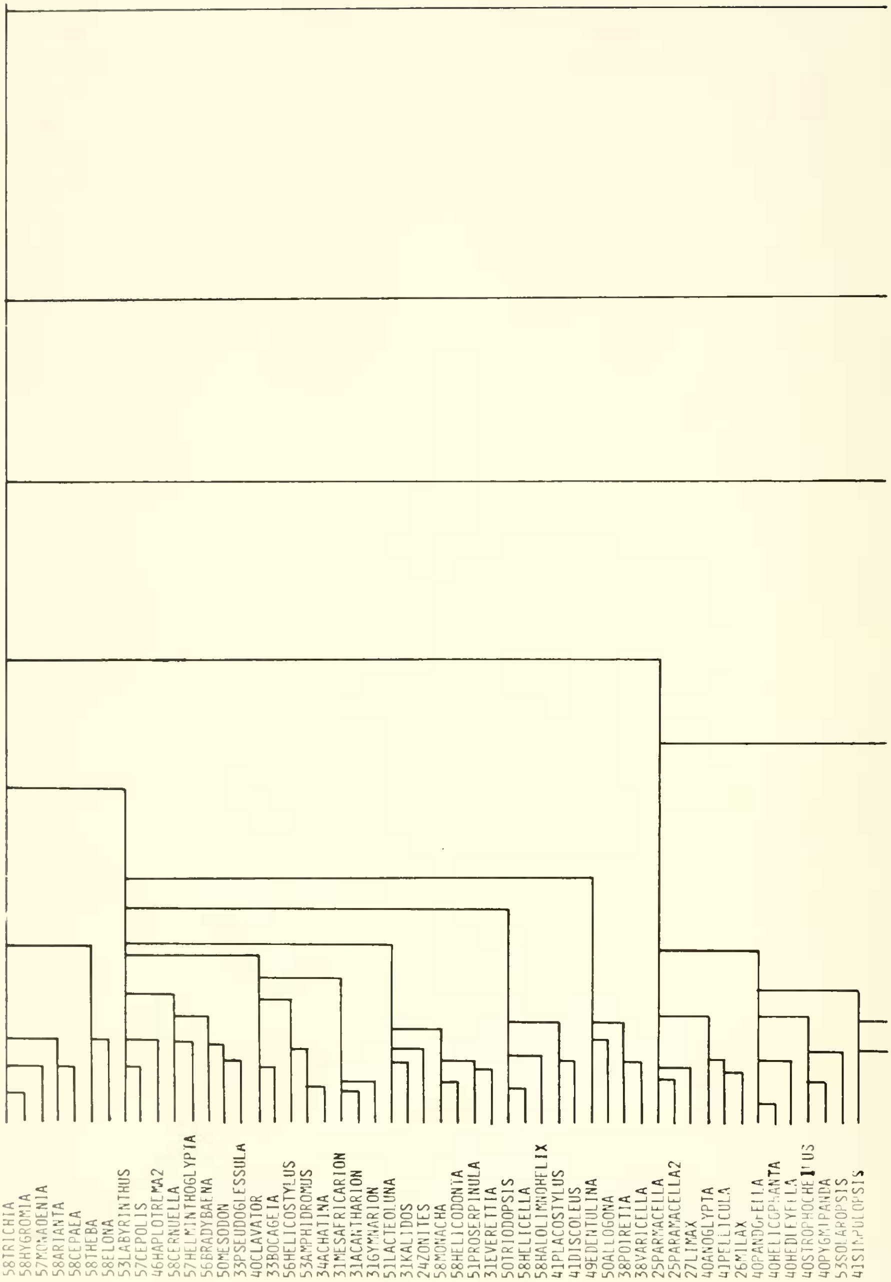
The Recent Achatinellidae are endemic to the Pacific Islands and along the western margin of the Pacific Ocean, although a few species have been introduced to the islands of the Indian Ocean (Cooke & Kondo, 1960). The Pitysinae, *Tubuaia* excepted, are endemic to the Austral Islands and the Achatinellinae are endemic to the Hawaiian Islands, whereas the Tornatellininae occur throughout the range of the family. One Carboniferous genus from Europe and North America has been attributed to the Achatinellidae (Solem & Yochelson, 1979). This attribution can be justified only on conchological characters, of which the evolutionary state is either dubious (shape, sculpture) or probably plesiomorphic (apertural teeth). The same arguments cast doubt on the affinities of *Protornatellina,* described from the Danian of North America. These genera are probably primitive, but their primitiveness does not at all imply monophyly with Recent achatinellids.

The digestive tract of the Achatinellidae is plesiomorphic for all characters considered in the various analyses. However, the important length of the intestine of *Partulina* was noticed by Pilsbry (1900a), and one can see (Fig. 16) that the intestine of *Achatinella lorata* is particularly broad. From the size of achatinellines, which are larger than in the other subfamilies, it might be supposed that these modifications in intestinal morphology are related to size increase, as previously discussed for all the Stylommatophora; but the increase in intestinal surface through an increase in intestinal diameter has been observed in *Achatinella* only, whereas the increase in surface through an increase in length seen in *Partulina* is more usual.

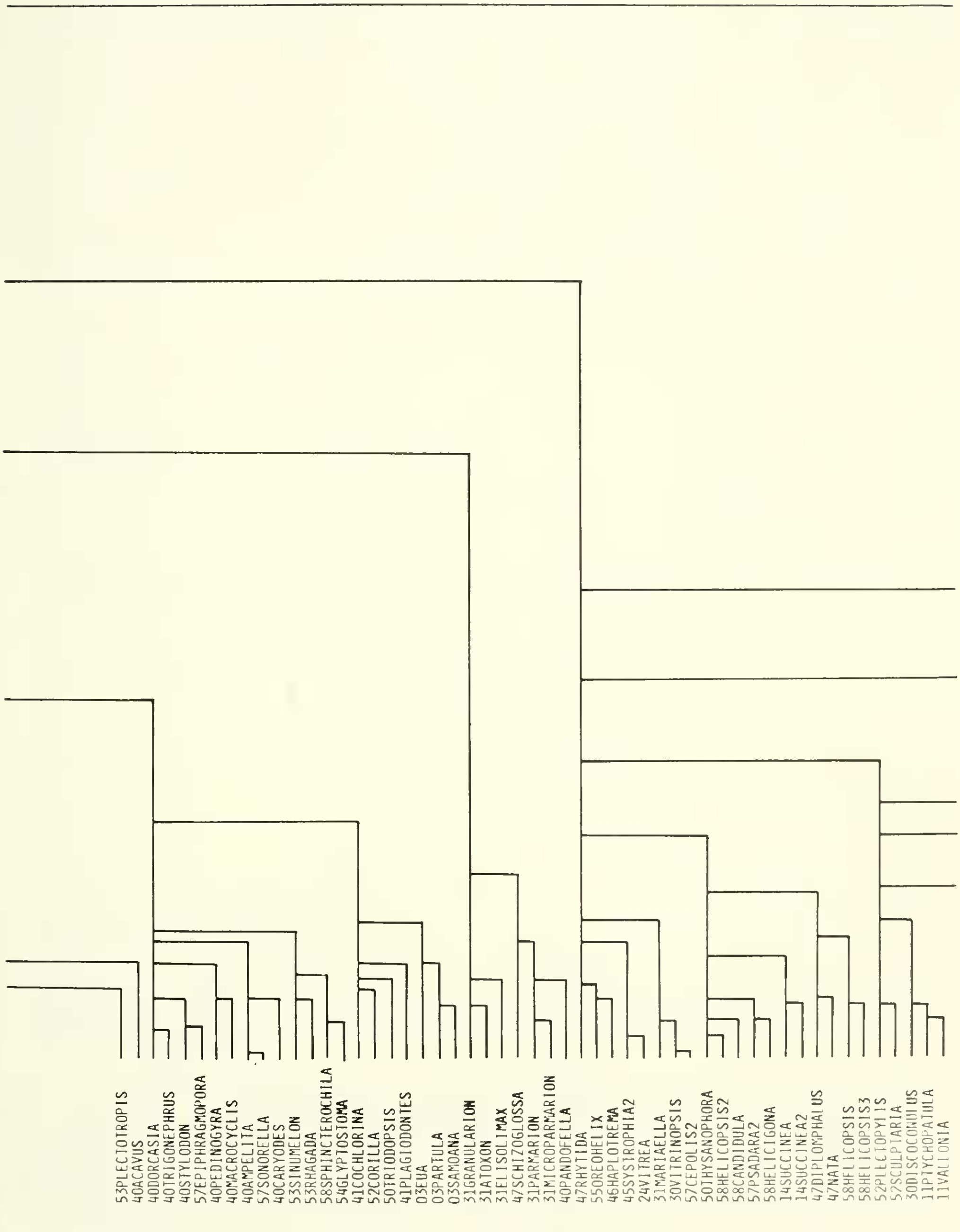
In achatinellids the cerebral commissure is never very long (CC1 absent). The right cerebro-pedal connective is never longer than the left (CPR1 absent). The right pleural ganglion is always closer to the right cerebral ganglion than to the right pedal ganglion (PLD2), whereas the position of the left pleural ganglion varies. The visceral ganglion is to the right of the median plane (VG1), and apparently fused with the right parietal ganglion (FG2).

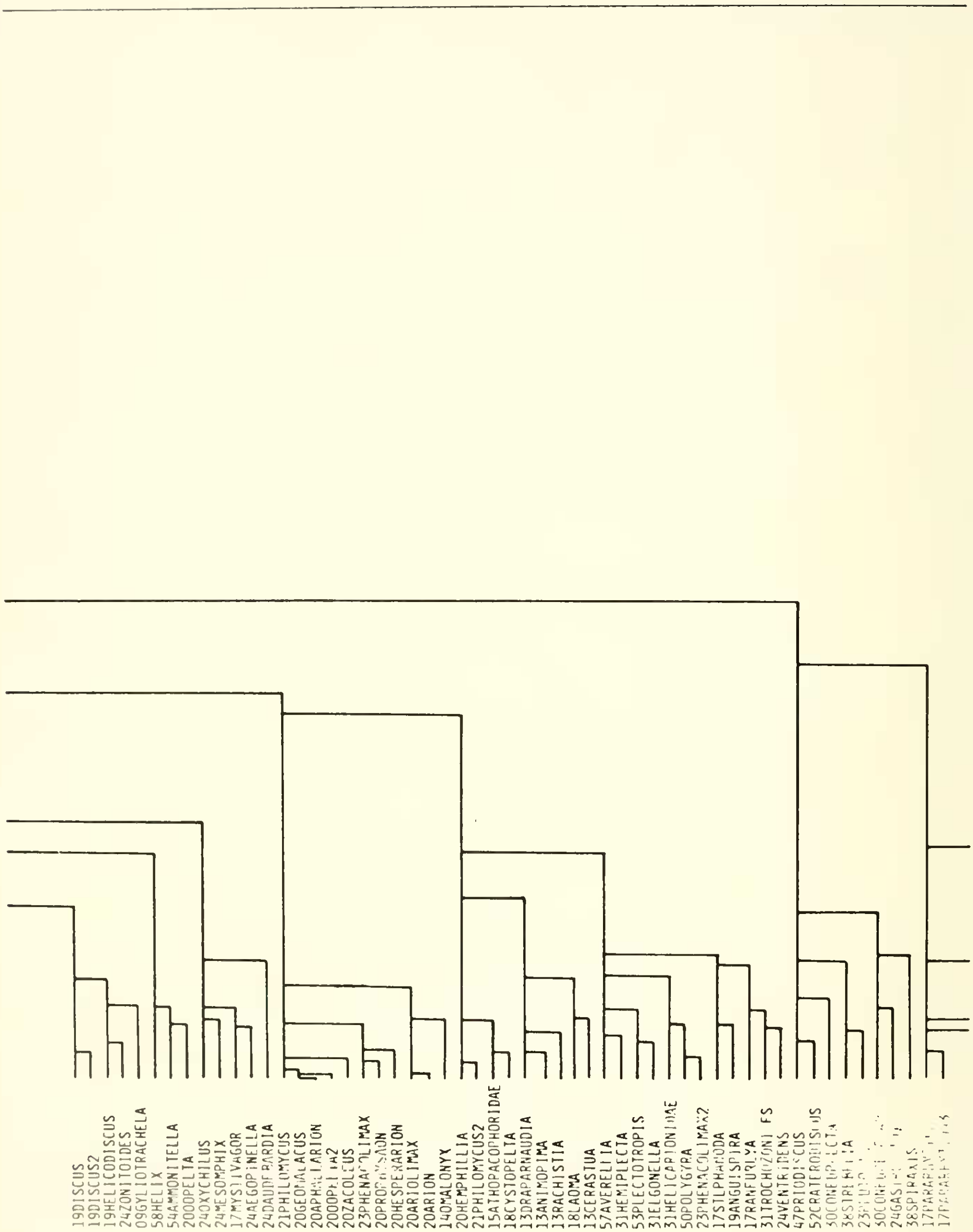
Association of the most plesiomorphic characters seen in the Achatinellidae provides the following hypothetical closest common ancestor (CCA): BM1 OC1 SC1 PS1 IL1 LR2′ UR1 RR1 CC2 CPD1 CPR2 PLD2 PLG1 VG1 PAD1 PAG1 FG2.

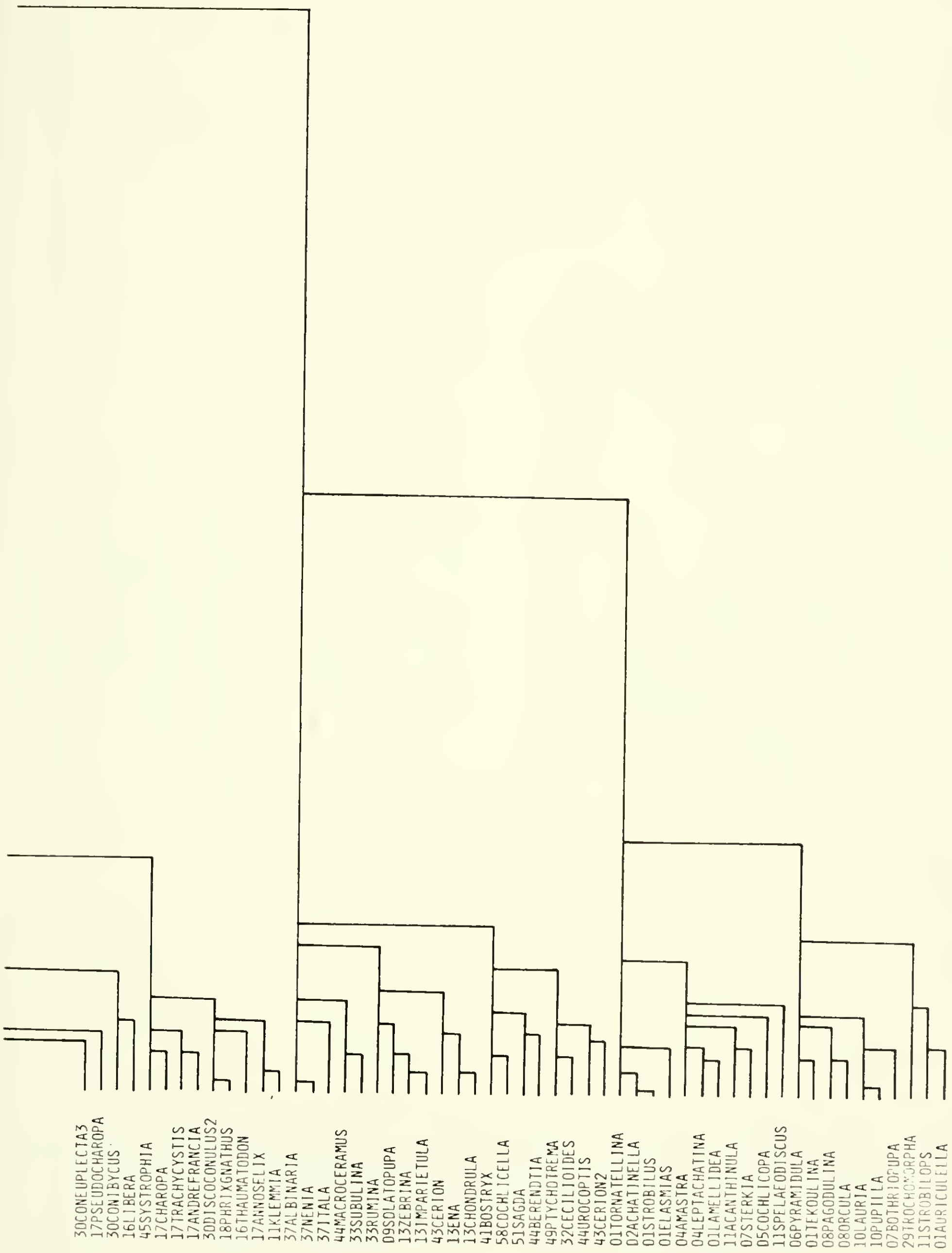
Valloniidae (+ Strobilopsidae) (Figs. 84–107, 110, 111): The Valloniidae are principally Holarctic; *Pupisoma s.l.* occurs in tropical regions, where probably it has been

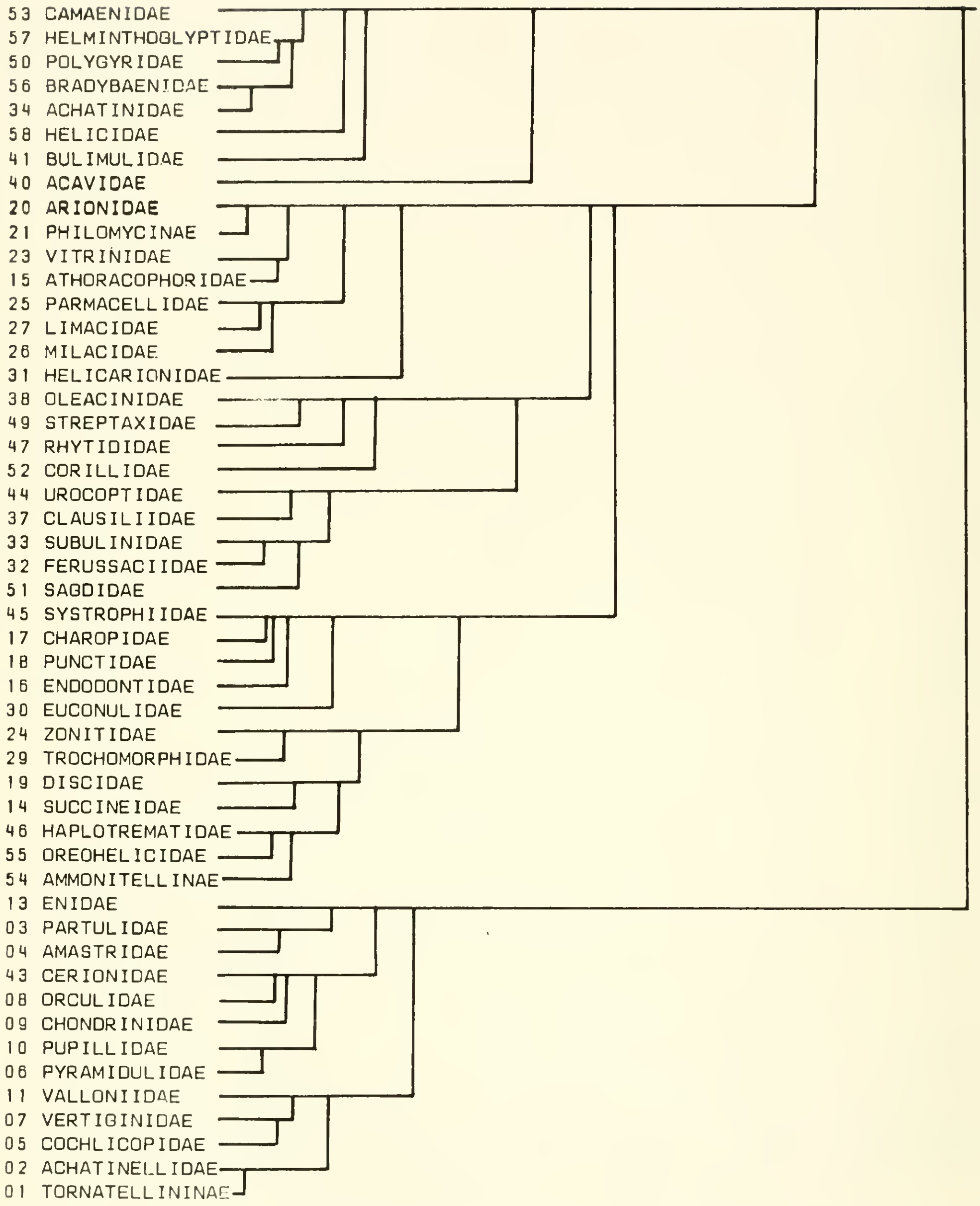


TEXT-FIG. 19. Phenetic ascending hierarchical classification of stylommatophoran species studied. Data, Appendix B, Figs. 1–704; limits of classes, Appendix D.


53PLECTOTROPIS
40ACAVUS
40DORCASIA
40TRIGONEPHRUS
40STYLODON
57EPIPHRAGMOPORA
40PEDINOGYRA
40MACROCYCLIS
40AMPELITA
57SONORELLA
40CARYODES
53SINUMELON
53RHAGADA
58SPHINCTEROCHILA
54GLYPTOSTOMA
41COCHLORINA
52CORILLA
50TRIODOPSIS
41PLAGIODONTES
03EUA
03PARTULA
03SAMOANA
31GRANULARION
31ATOXON
31ELISOLIMAX
47SCHIZOGLOSSA
31PARMARION
31MICROPARMARION
40PANDOFELLA
47RHYTIDA
55OREOHELIX
46HAPLOTREMA
45SYSTROPHIA2
24VITREA
31MARIAELLA
30VITRINOPSIS
57CEPOLIS2
50THYSANOPHORA
58HELICOPSIS2
58CANDIDULA
57PSADARA2
58HELICIGONA
14SUCCINEA
14SUCCINEA2
47DIPLOMPHALUS
47NATA
58HELICOPSIS
58HELICOPSIS3
52PLECTOPYLIS
52SCULPTARIA
30DISCOCONULUS
11PTYCHOPATULA
11VALLONIA


19DISCUS
19DISCUS2
19HELICODISCUS
24ZONITOIDES
09GYLIOTRACHELA
58HELIX
54AMMONITELLA
20OOPELTA
24OXYCHILUS
24MESOMPHIX
17MYSTIVAGOR
24AEGOPINELLA
24DAUDEBARDIA
21PHILOMYCUS
20GEOMALACUS
20APHALLARION
20OOPELTA2
20ZACOLEUS
23PHENACOLIMAX
20PROPHYSAON
20HESPERARION
20ARIOLIMAX
20ARION
14OMALONYX
20HEMPHILLIA
21PHILOMYCUS2
15ATHOPACOPHORIDAE
18CYSTOPELTA
13DRAPARNAUDIA
13ANIMOPIMA
13RACHISTIA
18LAOMA
13CERASTUA
57AVERELLIA
31HEMIPLECTA
53PLECTOTROPIS
31ELGONELLA
31HELICARIONIDAE
50POLYGYRA
23PHENACOLIMAX2
17STILPHANODA
19ANGUISPIRA
17RANFURLYA
31TROCHOZONI FS
24VENTRIDENS
47PRIODISCUS
52CRATEROHISCUS
30CONEUPLECTA
38STRE IA
23
30CONF
24GAS
38SPIRAXIS
17PARAPHA
17PARAPH


30CONEUPLECTA3
17PSEUDOCHAROPA
30CONIBYCUS
16LIBERA
45SYSTROPHIA
17CHAROPA
17TRACHYCYSTIS
17ANDREFRANCIA
30DISCOCONULUS2
18PHRIXGNATHUS
16THAUMATODON
17ANNOSELIX
11KLEMMIA
37ALBINARIA
37NENIA
37ITALA
44MACROCERAMUS
33SUBULINA
33RUMINA
09SOLATOPUPA
13ZEBRINA
13IMPARIETULA
43CERION
13ENA
13CHONDRULA
41BOSTRYX
58COCHLICELLA
51SAGDA
44BERENDTIA
49PTYCHOTREMA
32CECILIOIDES
44UROCOPTIS
43CERION2
01TORNATELLINA
02ACHATINELLA
01STROBILUS
01ELASMIAS
04AMASTRA
04LEPTACHATINA
01LAMELLIDEA
11ACANTHINULA
07STERKIA
05COCHLICOPA
11SPELAEODISCUS
06PYRAMIDULA
01TEKOULINA
08PAGODULINA
08ORCULA
10LAURIA
10PUPILLA
07BOTHRIOPUPA
29TROCHOMORPHA
11STROBILOPS
01AURICULELLA



TEXT-FIG. 20. Phenetic ascending hierarchical classification of stylommatophoran families. Data were obtained by summing indices representing each state, column by column, in each family, in data appendix used for classification shown in Text-fig. 19.

spread by man (Boss, 1982), and at least one "Strobilopsidae" occurs in New Guinea (Solem, 1968). The family ranges from the Paleocene to the Recent in Europe.

In the phenetic classification of the species, representatives of this family are dispersed as are all the Orthurethra (Text-fig. 19). The family is generally similar to the Vertiginidae and the Cochlicopidae, but the meaning of this similarity is doubtful in view of the great intrafamilial variability and the method used to construct the classification (Text-fig. 20).

Pilsbry (1948) proposed a monogeneric family Strobilopsidae based on the similarity of some conchological characters of *Strobilops* to those of the Pupillidae and Achatinellidae, i.e. upon purely phenetic conchological arguments. These characters might be plesiomorphic (apertural teeth); and because no anatomical character other than the plesiomorphic absence of fusion of the right parietal with the visceral ganglia allows distinction between the "Strobilopsidae" and other Valloniidae, I see no reason to maintain two distinct families.

Characters of the digestive tract are generally plesiomorphic, with the exception of a frequently short intestine and some gastric crop morphologies (gastric crop inflated in its median portion in *Vallonia,* possibly through paedomorphosis; and funnelform in *Ptychopatula*). A ureteric tube occurs in *Acanthinula* (UR2). The cerebral commissure and cerebro-pedal connectives are never long (CC2, CC3, CPD2, CPD3). The left cerebro-pedal connective is longer than the right, except in *Spermodea* (CPR1, CPR2, CPR3). The right pleural ganglion is always closer to the cerebral ganglion than to the pedal ganglion (PLD2), whereas the left pleural ganglion is in the same position only in *Strobilops.* As noted above, this genus differs from all other genera in its lack of fusion of the visceral and right parietal ganglia (FG1). The visceral ganglion is always on the right side (VG1).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR2′ UR1 RR1 CC2 CPD2 CPR1 PLD2 PLG1 VG1 PAD1 PAG1 FG1.

Pupillidae (Figs. 74–83): The family name is used here in its restricted sense, as defined by Zilch (1960; = Pupillinae + Lauriinae). Solem (1978) and Boss (1982) consider that the Orculidae, Chondrinidae and Vertiginidae should also be included. This position is comprehensible in view of the proximity of these families or of some of their members in the phenetic classifications (Text-figs. 19, 20).

Some Pupillinae are known from the Eocene in North America, and from the Oligocene in Europe. Recent taxa have been described from nearly everywhere in the world, but it will be impossible to evaluate the influence of accidental introductions as long as these very small and very variable animals remain unrevised.

In both genera studied here the median portion of the gastric crop is inflated (SC2). The cerebral commissure is not long (absence of CC1). The cerebro-pedal connectives are subequal in length (CPR2) and relatively long (CPD1, CPD2). The pleural ganglia are closer to the cerebral ganglia than to the pedal ganglia (CPD2, CPG2). The visceral ganglion is median (VG2). The left parietal ganglion is closer to the visceral ganglion than to the left pleural ganglion (PAG2), the former being apparently fused with the right parietal (FG2).

Character states of the CCA: BM1 OC1 SC2 PS1 IL1 LR2′ UR1 RR1 CC2 CPD1 CPR2 PLD2 PLG2 VG2 PAD1 PAG2 FG2.

Pyramidulidae (Figs. 49–51): The family is monogeneric or contains two genera if *Pleurodiscus,* the only genus of the "Pleurodiscidae," is included. No specimen of the latter could be found, and only one *Pyramidula* was dissected. The family is known from the European Eocene. In both phenetic classifications and in phylogenetic reconstructions (*v. infra*), the only pyramidulid seen is closer to the Pupillidae than to members of any other family: if my sampling were not so slight, I would not hesitate to consider the pyramidulids a subfamily of the Pupillidae.

The gastric crop is inflated in its median portion (SC2). The cerebral commissure is short (CC3), but the lateral connectives are long (CPD1) and subequal in length (CPR2). The pleural ganglia are closer to the cerebral ganglia than to the pedal ganglia (PLD2, PLG2). The visceral ganglion is on the right side (VG1), and the right parietal ganglion is closer to the right pleural ganglion than to the visceral ganglion (PAG1). The visceral ganglion seems fused with the right parietal ganglion (FG2).

Character states of *Pyramidula* (used as the CCA): BM1 OC1 SC2 PS1 IL1 LR2′ UR1 RR1 CC3 CPD1 CPR2 PLD2 PLG2 VG1 PAD 1 PAG1 FG2.

Chondrinidae (Figs. 65–73): The family ranges from the Eocene to the Recent in Europe. It is now mainly Holarctic and Oriental, but contains a few taxa of which the shell morphology is peculiar to the family, and that exhibit an interesting disjunct geographical distribution. This small group is composed of the African and Madagascan *Fauxulus,* the South American *Gibbulina* and *Ulpia,* and the Oriental, Australian and South African subfamily Hypselostomatinae. The great morphological difference between the two genera dissected in the family, *Gyliotrachela* (Hypselostomatinae) and *Solatopupa* (Chondrininae), makes the hypothesis of the phylogenetic unity of this small group worth testing (Text-fig. 19). Unfortunately, not enough material was available to me.

Taken together the two species dissected are close to the Cerionidae (probably not significant, *v. infra*), the Orculidae, Pupillidae and Pyramidulidae (Text-fig. 20).

The gastric crop is inflated in its median portion (SC2). The gastric pouch is separated from the gastric crop by a constriction (ES2′). The cerebral commissure is long to medium in length (CC1, CC2). The cerebro-pedal connectives are medium in length (CPD2); they are asymmetrical but their asymmetry is reversed in the two genera (CPR1 in *Solatopupa,* CPR3 in *Gyliotrachela*). The pleural ganglia are close to the cerebral ganglia in *Gyliotrachela* (PLD2, PLG2), and close to the pedal ganglia in *Solatopupa* (PLD1, PLG1). The left parietal ganglion is closer to the left pleural than to the visceral ganglion (PAG1). The latter seems fused with the right parietal ganglion (FG2).

Characters of the CCA: BM1 OC1 SC2 PS2′ IL1 LR2′ UR1 RR1 CC1 CPD2 CPR1 PLD1 PLG1 VG2 PAD1 PAG1 FG2.

Cochlicopidae (Figs. 43–45, 47, 48): The Cochlicopidae are Holarctic and include only four genera, of which only the most common species, *Cochlicopa lubrica,* was dissected. The family is known from the Paleocene in Europe and North America.

In both phenetic classifications, *Cochlicopa* is close to the Vertiginidae and Valloniidae (Text-figs. 19, 20). It is relatively close to the Amastridae, as in the commonly accepted classification and in the phylogenetic trees presented below, in the phenetic classification of the species but not in the phenetic classification of the families (sampling? Cochlicopidae + Amastridae = Cionellacea = Cochlicopacea in Boss, 1982).

In *Cochlicopa lubrica* the cerebral commissure and the lateral connectives are particularly long (CC1, CPD1). The asymmetry in the nerve ring is well marked (CPR3). The left parietal ganglion is closer to the visceral than to the left pleural ganglion (PAG2). The visceral ganglion, which lies on the right side (VG1), is appressed to the right parietal ganglion (FG2).

Considering that the characters used as characters of a CCA are here those of a species actually studied, and not of a reconstructed taxon, the number of plesiomorphic states is particularly high: BM1 OC1 SC1 PS1 IL1 LR2′ UR1 RR1 CC1 CPD2 CPR3 PLD1 PLG1 VG1 PAD1 PAG2 FG2.

Amastridae (Figs. 34–42): The Amastridae are endemic to the Hawaiian Islands. The family includes four to 12 genera depending on the authors (Boss, 1982; Zilch, 1959–1960), and is known from the Pleistocene of its modern distribution area only.

In the phenetic classification of the species, the Amastridae are close to *Cochlicopa* (the generally accepted position). They are farther away in the phenetic classification of the families, mainly owing to their larger size (Text-fig. 20).

All characters of the digestive tract are plesiomorphic, as in *Cochlicopa.* The cerebral commissure and lateral connectives are medium in length (CC2, CPD2). The left cerebro-pedal connective is longer than the right one (CPR3, CPR4). The pleural ganglia are near the pedal ganglia (PLG1, PLD1). The position of the visceral ganglion varies (VG1, VG3). The left parietal ganglion is appressed to the visceral ganglion (PAG3), and also touches the left pleural ganglion in *Amastra* (PAG4). The visceral ganglion seems fused with the right parietal ganglion (FG2).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR2′ UR1 RR1 CC2 CPD2 CPR3 PLD1 PLG1 VG1 PAD1 PAG3 FG2.

Vertiginidae (Figs. 52–55): The Vertiginidae range in Europe from the Paleocene to the Recent, and are now nearly ubiquitous. The two representatives of the family here dissected are closer to each other than to any other species in the phenetic classification of the species (Text-fig. 19). Together they are phenetically close to the Cochlicopidae and Valloniidae (Text-fig. 20).

All characters of the digestive tract are plesiomorphic. The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium in length (CPD2), the right one being longer than the left (CPR3). The pleural ganglia are closer to the cerebral ganglia than to the pedal ganglia (PLD2, PLG2). The visceral ganglion is on the right side of the median plane (VG1). The left parietal ganglion is closer to the visceral ganglion than to the left pleural ganglion (PAG2), and the right parietal ganglion seems fused with the visceral ganglion (FG2).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR2′ UR1 RR1 CC3 CPD2 CPR3 PLD2 PLG2 VG1 PAD1 PAG2 FG2.

Orculidae (Figs. 56–66): The family is known in Europe from the Paleocene, and now occurs eastward and southward to the Caucasus, Asia Minor and Ethiopia. In the phenetic classification of the families, it is curiously close to the Cerionidae, but also, and more expectedly, to the Chondrinidae, Pupillidae and Pyramidulidae (Text-fig. 20).

Pagodulina has an oesophageal crop associated with a cylindrical gastric crop, whereas *Orcula* has no oesophageal crop but a gastric crop inflated in its median portion. The kidney is relatively shorter in *Pagodulina* than in any other orthurethran dissected; but, as previously discussed, this relatively short length probably results from secondary lengthening of the distal region of the lung, rather than from plesiomorphy. In the two genera dissected the cerebral commissure is short (CC3). The cerebro-pedal connectives are medium in length (CPD2), the right one being longer than the left (CPR3). The pleural ganglia are close to the pedal ganglia in *Orcula* (PLD1, PLG1), but close to the cerebral ganglia in *Pagodulina* (PLD2, PLG2). The visceral ganglion is median (VG2). The left parietal ganglion is appressed to the visceral ganglion (PAG3), which seems fused with the right parietal ganglion (FG2).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR2′ UR1 RR1 CC3 PLD1 PLG1 VG2 PAD1 PAG3 FG2.

Partulidae (Figs. 25–33): The family Partulidae is endemic to Polynesia and Micronesia; no fossil is known. Following Pilsbry (1900a), authors have insisted on the primitiveness of the Partulidae, some even doubting their orthurethran affinities (Boss, 1982). Such opinions are not supported by any character here used or, as far as I know, by any genital character. However, one can understand the doubts raised by these authors in view of the phenetic classification of the species (Text-fig. 19), which shows both the homogeneity and the distinctness of the family. However, the Partulidae should be considered Orthurethra because: (1) their pallial complex has every orthurethran character state, including the great length of the kidney, which is here interpreted as a synapomorphy of the Orthurethra; (2) in the phenetic classification of the families (Text-fig. 20), they are closer to the Amastridae and Enidae than to any other stylommatophoran family.

In two of the three genera studied, *Eua* and *Partula,* the digestive tract is unique in having a gastric caecum. *Eua* also has a fleshy gastric appendix. As discussed above, I do not know whether these characters are apomorphic or plesiomorphic. The gastric crop is inflated in its median portion (SC2). The cerebral commissure is not very long in any of the three genera. The cerebro-pedal connectives are never very long (CPD1 absent), and the right one is always shorter than the left one (absence of CPR1). The pleural ganglia are close to the pedal ganglia (PLG1, PLD1). The visceral ganglion is median (VG2). The left parietal ganglion touches either the visceral ganglion only, or the visceral and the left pleural ganglia (PAG3, PAG4). The visceral ganglion seems fused with the right parietal (FG2).

Character states of the CCA: BM1 OC1 SC2 PS1 IL1 LR2′ UR1 RR1 CC2 CPD2 CPR 2 PLD1 PLG1 VG2 PAD1 PAG3 FG2.

Enidae (Figs. 108–146): The Enidae are mainly Palearctic. The subfamily Cerastuinae is principally East African, ranging from Arabia to South Africa; but it includes a few Oriental genera, and *Amimopina* in Queensland and *Draparnaudia* in New Caledonia and Vanuatu. The cerastuine affinities of the oldest genus known, *Procerastus* from the European Paleocene, are considered dubious by Zilch (1960). No other enid genus is known to be older than Miocene.

In the phenetic classification of the families (Text-fig. 20), the Enidae are closer to the Amastridae and Partulidae than to any other orthurethran family. This similarity may be attributed largely to the relatively large size of the animals in these three families. In the phenetic classification of the species (Text-fig. 19), the heterogeneity of the family as a whole and the homogeneity of the Cerastuinae on the one hand, and of the other Enidae on the other, is evident. Mordan (1984) cast doubt on the monophyly of the group. All characters here studied have either the same state in both subgroups, or are more apomorphic in the Cerastuinae. The pulmonary characters interpreted by Mordan as possible indications of paraphyly are those that were interpreted above as related to visceral mass shortening, which is common among the Stylommatophora although exceptional in the Orthurethra. These characters might constitute a synapomorphy of the subfamily, but cannot be used to reject the monophyly of the family.

An oesophageal crop is present in *Rachistia,* where it may related to the obvious shortening of the visceral mass (OC2). The gastric crop is inflated in its median portion in *Chondrula,* and separated from the gastric pouch by a constriction in this genus and in *Zebrina* (elongate shape). The intestine is short (IL1, IL2).

The Cerastuinae are unique in their general tendency to the formation of a ureteric tube, produced in part in *Rachistia* and *Amimopina* (UR2).

The cerebral commissure and the lateral connectives are never very long (CC1 and CPD1 absent). The left cerebro-pedal connective is always longer than the right one (CPR2, CPR3). The left pleural ganglion is closer to the left pedal ganglion (PLG1) in all the genera studied, whereas the right one is closer to the right cerebral ganglion in *Chondrula* and *Ena.* The left parietal ganglion always touches both the left pleural and the visceral ganglia (PAG4). In some genera the visceral ganglion is distinct from the right parietal ganglion (FG1).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR2′ RR1 CC2 CPD2 CPR2 PLD1 PLG1 VG1 PAD1 PAG4 FG1.

Non-orthurethran families

The non-orthurethran families show no synapomorphy among the characters described above: their hypothetical common closest ancestor (CCA) would be plesiomorphic for all characters. For convenience in presentation, families are here grouped in superfamilies that cannot be justified from familial descriptions, but only from the phylogenetic analysis presented below and resulting in the recognition of two suborders, the Dolichonephra and the Brachynephra.

Zonitoidea: Zonitidae (Figs. 235–258, 269–277): Some fossil shells from the Cretaceous of North America are generally thought probably to belong to the Zonitidae (Zilch, 1959–1960). In Europe the Zonitidae range from the Paleocene to the Recent. The family is now principally North American and circum-Mediterranean. The subfamily Godwininae occurs in the Hawaiian Islands (Baker, 1941), and the genus *Zonitoides* occurs throughout the Northern Hemisphere (introduced?).

The affinities of the Gastrodontinae with the Zonitidae are problematic; I have already underlined their similarity to the Systrophiidae in genital anatomy (Tillier, 1980). Furthermore, the gastrodontine *Ventridens* has a character found nowhere else but in the Systrophiidae, i.e. the position of the anterior duct of the digestive gland distinctly in front of the concave angle of the gastric pouch. The Gastrodontinae have the left parietal ganglion closer to the left pleural than to the visceral ganglion, unlike all other Zonitidae (PAG1, plesiomorphic); in *Gastrodonta* the right pleural ganglion is close to the right cerebral ganglion, as in systrophiids but unlike any Zonitidae examined (PLD2, apomorphic). With doubt I retain the Gastrodontinae in the Zonitidae because their CCA is closer to the CCA of the Zonitidae than to the CCA of the Systrophiidae.

In the phenetic classification of the families, the Zonitidae are close to the other unlimacized aulacopod families (Text-fig. 20).

The Zonitidae tend to be carnivorous, but not to such an extent as to have a cylindrical buccal mass, except in the daudebardiine slugs (BM1, BM2). There is no oesophageal crop (OC1). Gastric crop shape (SC1, SC2, SC3, SC2′), stomach shape (PS1, PS2, PS2′) and intestinal length (IL1 in the Gastrodontinae, IL2, IL3) are much more variable. The kidney is rather long (LR1, LR2; LR3 in the Gastrodontinae). The ureteric tube always extends as far as the pneumostome (UR4). The cerebral commissure is short (CC3), except in the Daudebardiinae, in which the occurrence of a long cerebral commissure (CC1) might be related to limacization and carnivory. The cerebro-pedal connectives are always long (CPD1), but the ratio of their lengths varies (CPR1, CPR2, CPR3; CPR4 in *Gastrodonta*). The visceral ganglion is on the right side (VG1), or median (VG2). The position of the right parietal ganglion varies (PAD1, PAD2). The left parietal ganglion is close to the left pleural ganglion in the Gastrodontinae (PAG1), but close to the visceral ganglion in the other Zonitidae (PAG2). The visceral ganglion might seem distinct (FG1) or fused with the right parietal ganglion (FG2).

When the Gastrodontinae are included in the Zonitidae, all the characters of the CCA but the occurrence of a ureteric tube are plesiomorphic: BM1 OC1 SC1 PS1 IL1 LR1 UR4 RR1 CC1 CPD1 CPR1 PLD1 PLG1 VG1 PAD1 PAG1 FG1.

Such a number of symplesiomorphies might result from para- or polyphyly of the Zonitidae, which really need a revision embracing the other zonitoid families. I suspect that, in its present definition, the family comprises several monophyletic groups, of which the sister groups might be among the other zonitoid families. This is why such small groups as the Limacidae, Milacidae, and Parmacellidae are here retained at the familial level.

Zonitoidea: Trochomorphidae (Figs. 278–282): Representatives of the family occur in Southeast Asia and the Western Pacific (from Japan to Vanuatu), and eastward to the Society Islands (Solem, 1959). Only one species, *Trochomorpha,* was dissected. It is phenetically close to the Zonitidae, which corresponds to the position assigned by Baker (1941), who considered the Trochomorphinae a subfamily of the Zonitidae (Text-fig. 20).

Trochomorpha is not carnivorous (BM1) and lacks an oesophageal crop (OC1). The gastric crop widens from oesophagus to stomach (SC2′) and the gastric pouch is differentiated (PS1). The intestine is short (IL2). The kidney is not very long (LR2), and is internally divided into two distinct regions (RR1). The ureteric tube is closed as far as the pneumostome (UR4). The cerebral commissure and the lateral connectives are short (CC3, CPD3), the latter being subequal in length (CPR2). Both pleural ganglia are closer to the cerebral ganglia than to the pedal ganglia (PLD2, PLG2). The visceral chain is compact (PAD2, PAG4), with the visceral ganglion in a median position (VG2) and distinct from the parietal ganglia (FG1).

Character states of the CCA (= character states of *Trochomorpha*): BM1 OC1 SC2′ PS1 IL2 LR2 UR4 RR1 CC3 CPD3 CPR2 PLD2 PLG2 VG2 PAD2 PAG4 FG1.

Zonitoidea: Euconulidae (Figs. 280, 283–295): The genus *Euconulus* is reported with doubt from the Upper Cretaceous, and with more certainty from the European and North American Paleocene (Zilch, 1959–1960). The present distribution of the Euconulidae is nearly world-wide, with maximum diversity in the Central and West Pacific and quasi-absence in the Australian region (Baker, 1938–1941).

In the phenetic classification of the families, the Euconulidae are close to the endodontoids *sensu* Solem, and to the Zonitidae (Text-fig. 20).

The Euconulidae are not carnivorous (BM1), and lack an oesophageal crop (OC1). The gastric crop is cylindrical (SC1), or narrows from oesophagus to stomach (SC3), the latter being differentiated (PS1) or not (PS2). The intestine is short to very short (IL2, IL3). The kidney is rather short (LR2, LR3), but a relatively long length can occur in relation to visceral mass shortening (LR1 in semislugs). A big renal lamella bearing transverse folds runs along and inside the rectal side of the kidney. The ureteric tube is closed as far as the pneumostome (UR4). The cerebral commissure is short (CC3). The lateral connectives are rather short (CPD2, CPD3) and shorter on the left side than on the right when asymmetric (CPR1). The right pleural ganglion is near the right cerebral ganglion (PLD2), whereas the position of the left pleural ganglion varies (PLD1, PLD2). The visceral ganglion is on the right side of the median plane (VG1). The left parietal ganglion is close to the left pleural ganglion (PAG1), whereas the right parietal ganglion seems fused with the visceral ganglion (PAD2, FG2).

Character states of the CCA: BM1 OC1 SC1 PS1 IL2 LR2 UR4 RR1 CC3 CPD2 CPR1 PLD2 PLG1 VG1 PAD2 PAG1 FG2.

Zonitoidea: Discidae (Figs. 184–194): To the extent that one can accept as criteria for familial attribution shell characters of which the direction of evolution is not known, the Discidae are known in the North American Carboniferous (Solem & Yochelson, 1979); other fossils attributable to the family are not known older than Paleocene in the same region and in Europe, where they still live.

Helicodiscus is here considered a discid, because: first, there are fewer differences between *Discus* and *Helicodiscus* than between some genera considered as Discidae *sensu stricto,* e.g. *Discus* and *Anguispira*; and second, *Helicodiscus* is closer to *Discus* than to any other genus of the Endodontoidea *sensu* Solem in the phenetic classification of the species dissected (Text-fig. 19). The Oriental *Stenopylis,* placed by Solem (1984) in his Helicodiscidae, is not necessarily involved: in my opinion, *Stenopylis* is an endodontoid by my definition (i.e. Solem's Endodontoidea, without the Discidae but with the Systrophiidae and Athoracophoridae), because its kidney is short and its ureter is partly open (UR2).

The Discidae, including *Helicodiscus,* are here considered zonitoids because they are much closer to the zonitids than to any endodontoid family in both the phenetic and phylogenetic classifications (Text-fig. 20, and below). This position might be wrong in various ways: the Helicodiscidae might be an endodontoid family, distinct from the Discidae, which are zonitoids; all the Discidae might be endodontoids. The North American *Anguispira* (Discidae) looks much more like the South American *Stephanoda*, which belongs to the Charopidae according to Solem (1982), than like any other of the Discidae or Zonitidae (Text-fig. 19).

The Discidae are not carnivorous (BM1) and lack an oesophageal crop (OC1). The gastric crop either is cylindrical (SC1) or widens from the oesophagus to the stomach (SC2′), the latter being differentiated (PS1). The intestine is rather short (IL2), except in *Anguispira*, in which its greater length (IL1) might be an effect of size increase. The kidney is also rather short (LR2, LR3). The internal kidney lamellae are little developed on the palatal surface of the kidney, whereas a very large lamella runs along the rectal border of the kidney. The ureter is closed as far as the pneumostome (UR4). The cerebral commissure is short (CC3) and the lateral connectives are long (CPD1). The left cerebro-pedal connective is shorter than the right one (CPR1). The pleural ganglia are both closer to the pedal ganglia than to the cerebral ganglia (PLD1, PLG1), but the right one is farther from the right pedal ganglion than the left one is from the left pedal ganglion. The visceral ganglion is on the right side of the median plane (VG1). The right parietal ganglion touches the visceral ganglion, both seeming fused in *Anguispira*. The left parietal ganglion is closer to the left pleural than to the visceral ganglion (PAG1).

Character states of the CCA: BM1 OC1 SC1 PS1 IL2 LR2 UR4 RR1 CC3 CPD1 CPR1 PLD1 PLG1 VG1 PAD2 PAG1 FG1.

Zonitoidea: Arionidae (+ Philomycidae) (Figs. 195–215, 217): The Arionidae and the Philomycinae share a synapomorphy, the annular kidney. The Philomycinae are distinct only in their more advanced slug condition, which results in a more compact nervous system among the characters used here. I can see no reason for separating them from the Arionidae at the familial level. They are North American and Oriental, whereas the other Arionidae are Holarctic and South African (*Oopelta*).

The South African genus *Oopelta* must be included in the Arionidae because it has a ring kidney, and resembles more the Arionidae than any other family even when this character state is disregarded (Text-fig. 19). This position is not so aberrant as one might suppose from a biogeographical point of view: several families (Enidae, Cerastuinae, Helicidae) seem to have invaded Africa from its northeast extremity, probably during the Miocene (*v. infra*), the epoch during which the family Arionidae appeared in the fossil record in Europe and in North America (Zilch, 1959–1960). The Arionidae have probably followed the same track, but became extinct in East Africa. Phenetically the Arionidae are close to the other aulacopod slugs (Text-fig. 20).

The Arionidae are not specialized in carnivory (BM1). The gastric crop is variable in shape (SC1, SC2, SC2′, SC3). The gastric pouch is differentiated (PS1), except in the semislug *Hemphillia* (PS2). The intestine is variable in length, but never very short (IL1, IL2, IL2′). The kidney is annular, with a ureteric tube reaching the pneumostome (UR4); its internal morphology has been described above. The cerebral commissure is long in *Oopelta* (CC1), and shorter in the Northern Hemisphere taxa (CC2). The cerebro-pedal connectives are medium to short in length (CPD2, CPD3). They are subequal in length, or the right one is longer than the left (CPR1, CPR2). The pleural ganglia are closer to the pedal ganglia than to the cerebral ganglia (PLD1, PLG1). The visceral ganglion is on the right side of the median plane (VG1) and seems fused either with the left parietal ganglion only (FG2′, *Oopelta*) or with both parietal ganglia (FG3).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR5 UR4 RR2 (RR1?) CC1 CPD2 CPR1 PLD1 PLG1 VG1 PAD2 PAG3 FG2′.

Zonitoidea: Parmacellidae (Figs. 259–262): The oldest fossils of this circum-Mediterranean family of slugs occur in the European Eocene. The species dissected here are phenetically close to the Limacidae and Milacidae (Text-figs. 19, 20).

The Parmacellidae are not carnivorous (BM1). The gastric crop is cylindrical (SC1) and the gastric pouch is dedifferentiated (PS2). The intestine is rather short (IL2). The kidney is compact, not internally differentiated (RR2), and the ureteric tube reaches the pneumostome (UR4). The cerebral commissure and the lateral connectives are long (CC1, CPD1), the latter being subequal in length (CPR2). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral chain is compact (PAD2, PAG4), but the visceral ganglion is distinct from the parietal ganglia (FG1) and median (VG2). Although the visceral chain is compact, its arrangement suggests derivation from a visceral chain in which the left parietal ganglion was closer to the left pleural than to the visceral ganglion.

Characters of the CCA: BM1 OC1 SC1 PS2 IL2 LR5 UR4 RR2 CC1 CPD1 CPR2 PLD1 PLG1 VG2 PAD2 PAG4 (PAG1?) FG1.

Zonitoidea: Limacidae (Figs. 263, 265–266): Limacid shells occur in the European Oligocene (Zilch, 1959–1960), and the family is now circum-Mediterranean (if one admits that *Agriolimax* = *Deroceras* has been introduced in North America as it was elsewhere).

The only species dissected, *Limax maximus,* differs from *Parmacella* in the shape of its gastric crop (SC2′), its very long intestine (IL2′: size effect?) and its shorter cerebral commissure and lateral connectives (CC3, CPD2).

Character states of the CCA (= character states of *Limax maximus*): BM1 OC1 SC2′ PS1 IL2′ LR5 UR4 RR2 CC3 CPD2 CPR2 PLD1 PLG1 VG2 PAD2 PAG4 FG1.

Zonitoidea: Milacidae (Figs. 264, 267–268): Milacid shells occur in the European Upper Eocene (Zilch, 1959–1960). The family includes only four genera, two of which are fossil, and is circum-Mediterranean.

The only significant difference allowing separation of *Milax* from *Limax* and *Parmacella* is among characters in the visceral chain, in which the visceral ganglion is on the left side of the median plane (VG3), and seems fused with the left parietal ganglion (FG2′). These differences might indicate different ancestral snails, but might also be due to the larger size of the semislug ancestors of *Milax.*

Character states of the CCA (= character states of *Milax*): BM1 OC1 SC2 PS2 IL2′ LR5 UR4 RR2 CC3 CPD2 CPR1 PLD1 PLG1 VG3 PAD2 PAG4 FG2′.

Helicoidea: Helicidae (Figs. 640–704): The Helicidae are known with certainty from the European Oligocene. Zilch (1959–1960) attributes with doubt a few Lower Eocene genera to the family. At present the Helicidae are principally European and circum-Mediterranean. The genus *Halolimnohelix,* from eastern Africa, belongs in the Helicidae, not in the Bradybaenidae: *Halolimnohelix (H.) sericata lejeunei* has finger-shaped multifid glands similar to those classically used as a synapomorphy of the Helicidae. Seemingly no known African helicoid has an amatorial organ formed by a muscular trunk terminated by a sagittiform glandular formation, as occurs in the Bradybaenidae (e.g. Pilsbry, 1919).

As might be expected, the Helicidae are phenetically close to the Camaenidae, Bradybaenidae, Helminthoglyptidae and Polygyridae (classical position); but less expectedly, they are also close to the Achatinidae and Bulimulidae (Text-figs. 19, 20).

Among the character states used here only the absence of internal differentiation of the kidney, the position of the contact of the left parietal ganglion with the visceral ganglion and the closure of the ureteric tube at least as far as the recto-renal angle are synapomorphous for all helicids (RR2, PAG4, UR3). The helicids are never carnivorous (BM1), and often have an oesophageal crop (OC2, OC3, OC4). The kidney is never very short (LR1, LR2, LR3). The pleural ganglia are near the pedal ganglia (PLD1, PLG1). The visceral ganglion is generally either median or on the left side (VG2, VG3).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR1 UR3 RR2 CC1 CPD1 CPR1 PLD1 PLG1 VG1 PAD1 PAG3 FG1.

Although classically considered "the most highly organized Helices upon the globe," probably because they are the dominant family in Western Europe (Taylor, 1900), the Helicidae have a greater number of plesiomorphic characters than nearly any other non-orthurethran family. As in the case of the Zonitidae, this might result from para- or polyphyly. Among those genera dissected here two, *Helicodonta* and *Cochlicella,* show such a morphology of the amatorial organ that no one would hesitate to classify them among the helminthoglyptids, if they occured in North America (Germain, 1930; Pilsbry, 1940). Within the family classification is at best confused. The only contribution possible here is the proposal to restrict the Helicellinae, of which the monophyly has been long contested (Watson, 1922; Shileyko, 1978c), to genera having a ureteric appendage along the rectum, as described above.

Helicoidea: Helminthoglyptidae (Figs. 607–639): The oldest genera that Zilch (1959–1960) attributes to the helminthoglyptids occur in the Cretaceous (*Mesoglypterpes*) and the Upper Paleocene (*Glypterpes*) of North America. Representatives of the family live principally in western North America, Mexico and Central America. The genus *Epiphragmopora* extends southward in western South America to Argentina.

The Central American and Caribbean Thysanophorinae are here included in the Helminthoglyptidae, not in the Polygyridae, for two reasons. First, *Thysanophora* is phenetically closer to some Helicidae than to any Polygyridae (the distinction between Helicidae and Helminthoglyptidae is often impossible without geographical data, as discussed above and below). Second, the ureteric tube is not closed as far as the pneumostome in *Thysanophora,* as seen in about half of the dissected Helminthoglyptidae but in none of the Polygyridae (Fig. 610).

The tropical South American genus *Psadara* is included in the Cepolinae (I formerly supported its classical position in the Camaenidae, Tillier, 1980) for two reasons. First, *Psadara* is phenetically closer to *Thysanophora* and to some Helicidae than to any of the Camaenidae (Text-fig. 19). The arrangement of organs in *Cepolis maynardi* looks very much like that in *Psadara* (Figs. 621, 622). Second, both *Psadara* and *Cepolis* have a kidney longer than that in any other non-limacized non-orthurethran snail (synapomorphy; Figs. 616, 618).

The Cepolinae and Thysanophorinae might form a single subfamily (or even a family distinct from the Helminthoglyptidae, the inclusion of the Cepolinae in the latter being not obvious: Pilsbry, 1940). However, I consider that better knowledge of these groups than mine is necessary to support this unity.

Sonorella is closer to *Epiphragmopora* than to any other helicoid in the phenetic classification of species (Text-fig. 19). This similarity might justify the inclusion of the Sonorellinae in the Helminthoglyptidae, about which Pilsbry himself (1940) was unsure. On the other hand, the Helminthoglyptidae are closer to the Polygyridae than to any other family of the Helicacoidea *sensu stricto* in the phenetic classification of the families (Text-fig. 20), and it would be worth testing the monophyly of the Polygyridae and of the Sonorellinae (Helicacoidea *sensu stricto* = Helicidae, Helminthoglyptidae, Bradybaenidae).

The Helminthoglyptidae and Helicidae are distinguished by remarkably few character states. In the former the cerebral commissure is always very short (not always so in the Helicidae); the kidney is internally differentiated in at least a few genera; the left parietal ganglion always touches the visceral ganglion (it does not in a single dissected helicid genus, *Sphincterochila*). Perhaps these differences, of which none is absolute (no synapomorphy of either of the families), would not resist further sampling, which might possibly reveal amphi-Atlantic monophyletic groups.

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR1 UR3 RR1 CC3 CPD1 CPR1 PLD1 PLG1 VG2 PAD2 PAG4 FG1.

Helicoidea: Bradybaenidae (Figs. 587–594): The Bradybaenidae can be defined by the morphology of their amatorial organ, formed by a muscular trunk, issuing from the vagina, on which numerous acini forming a sagittiform apical mass are inserted. The same structure occurs in the Dyakiinae (Helicarionidae?); this point will be discussed further. This definition excludes the African *Halolimnohelix* from the family, as discussed above.

When so defined the Bradybaenidae are principally Oriental and rarefy westward, only the genus *Bradybaena* reaching Western Europe. Fossils are known from the Chinese Pliocene (*Cathaica*); the purely anatomical definition of this family makes its earlier occurrence possible, and some of the fossil helicoids might belong to the Bradybaenidae.

In the phenetic classifications of the species and families, the Bradybaenidae are close to other helicoids (Text-figs. 19, 20).

No bradybaenid is carnivorous (BM1). The two genera dissected have a large oesophageal crop (OC3, OC4), which is either cylindrical or inflated in its median portion (SC1, SC2; the latter state is an effect of shape in *Helicostylus*). The intestine is long (IL1). The kidney is long to very long (LR1, LR2′), such considerable relative lengths being possibly an effect of visceral mass and lung shortening. The ureteric tube is closed as far as the pneumostome (UR4). The kidney is internally differentiated (RR1). The cerebral commissure is very short (CC3). The cerebro-pedal connectives are rather long (CPD1, CPD2) and subequal in length (CPR2). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is either median or on the left side (VG2, VG3). The right parietal ganglion touches the visceral ganglion (PAD2), and the left parietal ganglion is in contact with both the visceral and the left pleural ganglia (PAG4). Apparent fusion of the left parietal and visceral ganglia occurs in one case.

Character states of the CCA: BM1 OC3 SC1 PS1 IL1 LR1 UR4 RR1 CC3 CPD1 CPR2 PLD1 PLG1 VG2 PAD2 PAG4 FG1.

Helicoidea: Polygyridae (Figs. 577–586): The Polygyridae occur in the Miocene of North America, where most genera are still endemic; the Cretaceous fossil attributed to the Polygyridae by Zilch (1959–1960) belongs to the Ammonitellinae (Solem, *in litt.*). The North American genus *Polygyra* extends to Cuba in the West Indies (Boss, 1982).

The species dissected here are dispersed, as are the other helicoids, in the phenetic classification of the species (Text-fig. 19), and the family is phenetically close to the other helicoid families (Text-fig. 20).

No polygyrid is carnivorous (BM1). An oesophageal crop might be present (OC1, OC2, OC3). The shape of the gastric crop and gastric pouch is variable, but the gastric pouch is never reduced (PS2 absent). The lengths of the intestine and of the kidney are variable (IL2, IL2′, LR1, LR2, LR3). The ureteric tube is always closed as far as the pneumostome (UR4). There are two morphological regions in the kidney (RR1). The cerebral commissure is short (CC3). The cerebro-pedal connectives vary in length, but the right one is longer than the left one in the species dissected (CPR3). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is median or on the left side (VG2, VG3). The right parietal ganglion touches the visceral ganglion (PAD2). The left parietal ganglion seems fused with the visceral ganglion, and touches the left pleural ganglion (PAG4).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR1 UR4 RR1 CC3 CPD1 CPR2 PLD1 PLG1 VG2 PAD2 PAG4 FG2′.

Helicoidea: Camaenidae (Figs. 556–576): The Camaenidae are classically defined among the helicoids *s.s.* by the absence of an amatorial organ. Even if this absence is apomorphic, which is likely, it is also shown by the Polygyridae and Sonorellinae in the same group. The definition and classification of the Camaenidae are thus far from being secure. In its present definition, the family seems to occur in the Cretaceous of North America (*Hodopeus*) to the extent that shell characters are reliable in the helicoids. It is now West Indian and Oriental, with representatives reaching Australia on one side and possibly South America on the other side (*v. infra*).

The Oriental genus *Plectotropis* is here placed among the Camaenidae, as suggested by Solem (1966a) on a conchological basis: *Plectotropis goniocheila* has no amatorial organ.

The position of the American camaenids, *Pleurodonte* and the related Antillean genera on one hand, and the South American genera *Solaropsis, Labyrinthus* and *Isomeria* on the other hand, is far more problematic. First, *Solaropsis* and *Labyrinthus* are very similar in the general arrangement of their organs (Figs. 556, 559), and in the aspect of living animals (Tillier, 1980). Both genera have a character unique among the Stylommatophora dissected, i.e. the typhlosole that issues from the anterior duct of the digestive gland is more developed than the one issuing from the posterior duct. Both genera live in the Amazonian region, but occupy well-defined and different niches (Tillier, 1980), and convergence is unlikely. Secondly, the lung and kidney of *Solaropsis* have a peculiar arrangement, which reminds one more of the Acavidae than of the Camaenidae (Tillier, 1980). The same organs are more camaenid-like in *Labyrinthus,* although the kidney is longer than in any camaenid, as in *Solaropsis.* Thirdly, *Labyrinthus* is very similar to *Pleurodonte,* although the latter does not show the same morphology of the typhlosoles, and *Pleurodonte* is itself very similar to the Australian camaenid *Sinumelon* (not depicted here); the genital anatomy and its pattern of variation are similar in these two genera (Solem, pers. comm.). Even if we suppose that the group of *Solaropsis* does not belong to the Camaenidae, the position of the *Pleurodonte* group remains problematic owing to its similarity to *Labyrinthus.* This is why the family is here preserved in its larger definition, which can easily be justified by the absence of synapomorphy whatever solution is adopted. However, the hypothesis that the *Pleurodonte* group belongs to, or is directly related to the Cepolinae, Thysanophorinae or Sonorellinae should be carefully evaluated.

The Camaenidae are not carnivorous (BM1). All species dissected have an oesophageal crop (OC2, OC3, OC4). The gastric crop is cylindrical (SC1), except in *Sinumelon* where its widening toward the stomach (SC2′) might be related to its very short length. The intestine varies in length (IL1, IL2, IL2′), but is never very short. The kidney is rather long (LR1, LR2). The ureteric tube is closed as far as the pneumostome (UR4), except in *Solaropsis* (UR3). The kidney has two internal regions in all the Oriental camaenids dissected (RR1), but in no Neotropical one (RR2). The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium in length (CPD2). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The position of the visceral ganglion varies (median or on the left in all Oriental camaenids: VG2, VG3). The visceral chain is compact, and the visceral ganglion might look fused with the left parietal ganglion (PAD2, PAG4, FG1 or FG2′).

Character states of the CCA: BM1 OC2 SC1 PS1 IL1 LR1 UR3 (UR4 if *Solaropsis* is omitted) RR1 (RR2 for the American camaenids) CC3 CPD2 CPR1 PLD1 PLG1 VG1 (VG2 in Oriental camaenids) FG1 (FG3 for American camaenids).

Helicoidea: Sagdidae (Figs. 600–606): Baker (1962) moved the Sagdidae, which occur in the Greater Antilles and in southeastern North America, from the Polygyracea to the Achatinacea. His arguments are based on the geographical distribution, the carnivorous diet and the incompletely closed ureteric tube, features which unite, in his opinion, the Sagdidae and the Spiraxidae, which he considers as belonging to the achatinoids. The Spiraxidae are here considered oleacinids (*v. infra*). The Sagdidae are closer to the helicoids than to the oleacinids in the phenetic classification of the species (Text-fig. 19), whereas they are closer to the oleacinids in the phenetic classification of the families (Text-fig. 20). Three further pieces of evidence bear on these points. First, the Oleacinidae and the Spiraxinae have a short kidney (apomorphic) and a visceral ganglion distinct from the parietal ganglia (plesiomorphic). Second, the Sagdidae have a long kidney (plesiomorphic; except in *Sagda*, in which the relatively short length of the kidney is related to the lengthening of all other organs, including the lung roof) and a visceral ganglion that seems fused with the left parietal ganglion (apomorphic). Third, the lateral penial appendix of the Sagdidae closely resembles the amatorial organ of the Helminthoglyptidae, and I suspect that it represents the same organ, but shifted from the vagina to the penis.

Even if the amatorial organ is plesiomorphic in the Stylommatophora, or if the penial appendix of the Sagdidae is not homologous with the amatorial organ of the Helminthoglyptidae, there is one synapomorphy with the latter and no synapomorphy with the oleacinids. Consequently, it might be more reasonable to include the Sagdidae in the helicoids beside the Polygyridae and the Helminthoglyptidae (*v. infra*) rather than in the achatinoids, which include the oleacinids in the classification presented here, beside the Spiraxinae as proposed by Baker.

Although the Sagdidae are carnivorous, their buccal mass is not particularly lengthened (BM1). They do not have an oesophageal crop (OC1). The gastric crop is inflated in its median portion (SC2) or widens toward the stomach (SC3). The intestine is short (IL2) and the kidney is long (LR1), except in *Sagda* where a long intestine and a short kidney result from visceral mass lengthening (lung three whorls long). The ureteric tube is closed as far as the pneumostome (UR4). In *Sagda* it is prolonged by a transverse caecum above the pneumostome, as in *Succinea* (Fig. 224). The kidney is not differentiated internally (RR2). The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium in length, and subequal (CPD2, CPR2). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is median or on the left side (VG2, VG3), and seems fused with the left parietal ganglion (FG2′), which touches the left pleural ganglion (PAG4). The right parietal ganglion is close to the right pleural ganglion (PAD2).

Character states of the CCA: BM1 OC1 SC2 PS1 IL2 LR1 UR4 RR2 CC3 CPD2 CPR2 PLD1 PLG1 VG2 PAD2 PAG4 FG2′.

Helicoidea: Haplotrematidae (Figs. 595–599): The family Haplotrematidae is endemic to western North America, Central America and the northern Caribbean region. They are close to the Oreohelicinae in the phenetic classifications (Text-figs. 19, 20).

The Haplotrematidae are carnivorous, but their buccal mass is not particularly developed (BM1). They do not have an oesophageal crop (OC1). The gastric crop is cylindrical and the gastric pouch is differentiated (SC1, PS1). The intestine is rather long (IL1). The kidney is rather short (LR2) and internally differentiated into two distinct regions (RR1). The ureteric tube is closed as far as the pneumostome (UR4). The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium in length (CPD2) and the right one is longer than the left (CPR3). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is median (VG2) and seems fused with the left parietal ganglion (FG2′). The visceral chain is short, but the left parietal ganglion does not touch the left pleural ganglion (PAD2, PAG3).

Character states of the CCA: BM1 OC1 SC1 IL1 LR2 UR4 RR1 CC3 CPD2 CPR3 PLD1 PLG1 VG2 PAD2 PAG3 FG2′.

Helicoidea: Helicarionidae (Figs. 296–340): The contents of this taxon are those indicated by Zilch (1959–1960), i.e. with the Euconulidae excluded. The Euconulidae and the Helicarionidae have an aulacopod foot and sigmoid radular teeth tending to be very numerous (Baker, 1938, 1940, 1941), but the aulacopody might be convergent through paedomorphosis, and the shape and number of the radular teeth might be convergent through diet: at least all the Helicarionidae seen feeding ate macromycetes (observed by C. Blanc in Madagascar, by E. Binder in West Africa and by me in New Caledonia).

The Helicarionidae occur in tropical regions, except South America and the Central Pacific Islands. The groups defined by Solem (1966a) within the Helicarionidae might be monophyletic, but I doubt that the whole family forms a monophyletic group although I cannot justify rigorously this opinion. The representatives of the family are very dispersed in the phenetic classification of the species (Text-fig. 19), and the family is close to other aulacopod groups in the phenetic classification of the families (convergence?; Text-fig. 20).

The subfamily Dyakiinae is peculiar in its general and genital morphology (Solem, 1966a). In this subfamily the amatorial apparatus is similar to that in the Bradybaenidae; the Dyakiinae and Bradybaenidae possibly form a monophyletic group. Although raising further questions, this remark supports the placement of the helicarionids among the Helicoidea, already proposed by Schileyko (1978a). However, it is unlikely that the amatorial organ of the Urocyclinae and Gymnarioninae is homologous with that of the Helicoidea, because the hypothesis of its secondary differentiation seems well documented (Van Mol, 1970; Binder & Tillier, 1985).

All the Helicarionidae have an aulacopod foot. Their buccal mass is not elongated (BM1), and the snails lack an oesophageal crop (OC1). The homology of the crop of semislugs and slugs (OC3, OC4) is dubious (*v. supra* and Tillier, 1984a). The intestine is never very long (IL1, IL2). The kidney is long (LR1). Most internal renal lamellae are not very developed, but a large, transversely folded lamella runs along the rectal side of the kidney. The ureteric tube is closed as far as the pneumostome (UR4). The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium to short in length (CPD2, CPD3), subequal in length (CPR2), or the right one is longer than the left (CPR3). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1), except in the West African semislug *Granularion* (PLD2, PLG2). The position of the visceral ganglion varies (VG1, VG2, VG3). The right parietal ganglion is always closer to the visceral ganglion than to the right pleural ganglion (PAD2). The left parietal ganglion touches either the visceral ganglion only (PAG3) or both the visceral and left pleural ganglia (PAG4). Generally the visceral ganglion is distinct from the parietal ganglia (FG1), but it seems fused with the right parietal ganglion in the ariophantine *Hemiplecta* (FG2), and seems fused with the left parietal ganglion in the parmarionine slug *Parmarion* (FG3).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR1 UR4 RR1 CC3 CPD2 CPR2 PLD1 PLG1 VG1 PAD2 PAG3 FG1.

Helicoidea: Vitrinidae (Figs. 228–234): The earliest genus attributed to the Vitrinidae is *Provitrina*, described from the European Paleocene. Shells assigned to Recent genera occur in the European Oligocene (Zilch, 1959–1960). At present the family is principally Holarctic, and includes a few representatives in east and northeast Africa and in the Central Pacific islands.

All the Vitrinidae have a visceral mass shortened or even incorporated in the pedal cavity. Their similarity to the Helicarionidae is obvious, and their position close to some Helicarionidae in the phenetic classification of the species (Text-fig. 19) reminds one of Schileyko's assessment (1978a) of their affinities. They are near the families of aulacopod slugs in the phenetic classification of the families (Text-fig. 20).

These animals are carnivorous, but the buccal mass is elongated in the slug *Plutonia* only (BM1, BM2). There is no oesophageal crop (OC1). The gastric crop varies in shape (SC1, SC2, SC2′). The gastric pouch is differentiated in both the snails and semislugs

(PS1), but dedifferentiated in *Plutonia* (PS2, carnivory). The intestine is short (IL2). The ureteric tube is closed as far as the pneumostome (UR4). The kidney is not differentiated internally (RR2), and has a thick internal lamella along its rectal side. The cerebral commissure is short (CC3). The cerebropedal connectives are short (CPD3), except in *Plutonia* where their greater length might be related to the development of the buccal mass (carnivory, CPD2). The right cerebropedal connective is longer than the left (CPR3). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is median (VG2) or on the left side (VG3, *Plutonia*). The parietal ganglia are closer to the visceral ganglion than to the pleural ganglia (PAD2, PAG3). The visceral ganglion seems fused with the right parietal ganglion in *Phenacolimax* (FG2), and with the left parietal ganglion in *Plutonia* (FG3).

Character states of the CCA: BM1 OC1 PS1 IL2 LR5 UR4 RR2 CC3 CPD2 CPR3 PLD1 PLG1 VG2 PAD2 PAG3 FG1.

Plutonia is very similar to *Milax* not only in its external morphology (tail carinate), but also in the arrangement of its nervous system. However, I do not think that close affinity must be asserted, principally because the kidney of *Milax* does not have a thick internal lamella running along its rectal side.

Achatinoidea: Succineidae (Figs. 221–227): The Succineidae are world-wide, and some occur in the European Paleocene (Zilch, 1959–1960). Phenetically, they are close to the Discidae, Haplotrematidae and Oreohelicidae (Ammonitellinae included) despite their elongate shape (Text-fig. 20). I have already discussed and rejected their placement with the Athoracophoridae in a suborder Heterurethra (Tillier, 1984a).

The Succineidae are not carnivorous (BM1), and lack an oesophageal crop (OC1). The gastric crop is cylindrical (SC1), except in the slug *Omalonyx* (SC2′). The stomach might be dedifferentiated (PS1, PS2), a caecum being developed in compensation (Tillier, 1984a). The intestine is rather long in snails (IL1), and shorter in slugs (IL2). The kidney is short (LR3) but is transversely elongate (heterurethry). The ureteric tube is closed as far as the pneumostome, and is prolonged by a caecum across the pneumostome roof in some species of *Succinea* (Fig. 224). The kidney is not differentiated internally (RR2). The cerebral commissure is medium in length (CC2). The cerebro-pedal connectives are short (CPD3), the left one being shorter than the right (CPR1). The pleural ganglia are near the pedal ganglia (PLD1, PLG1). The visceral ganglion is median (VG2) and seems fused with both the parietal ganglia (FG3). The visceral chain is compact (PAD2, PAG4).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR3 UR4 RR2 CC2 CPD3 CPR1 PLD1 PLG1 VG2 PAD2 PAG4 FG3.

Achatinoidea: Ferussaclidae (Figs. 356, 358–360): The Recent genus *Coilostele* occurs in the European Lower Eocene (Zilch, 1959–1960). The present distribution of the family is circum-Mediterranean, African, Oriental and Neotropical.

Only one species, *Cecilioides acicula,* was dissected. It is close to the Subulinidae, but also to the Urocoptidae and Clausiliidae in the phenetic classification of the families. As mentioned above, the Ferussaciidae and the Succineidae both exhibit heterurethry (apomorphic) and aulacopody (apomorphic), but also two procerebral commissures (plesiomorphic; Watson, 1928). Furthermore the penial retractor muscle in *Cecilioides* is a branch of the columellar retractor, which probably corresponds to the ancestral condition in the Succineidae (Tillier, 1984a).

Cecilioides is not carnivorous (BM1) and does not have an oesophageal crop (OC1). The median portion of the gastric crop is inflated (SC2) and a constriction separates the gastric crop from the gastric pouch (PS2′). The intestine is short (IL2). The kidney is very short (LR4) but transversely elongate such that its primitively visceral side runs along the rectum. The internal renal lamellae are reduced to a series of lamellae perpendicular to the rectal border and present only on the pulmonary surface of the kidney; their arrangement reminds one of that in the Succineidae (small lamellae perpendicular to the rectal border) and in the Oleacinidae (lamellae absent from the palatal surface of the kidney) (Figs. 358, 225, 367). The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium and subequal in length (CPD2, CPR2). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The parietal ganglia touch the visceral ganglion (PAD2, PAG3) but are distinct from them (FG1). The visceral ganglion is on the right side (VG1).

Character states of the CCA (= character states observed in *Cecilioides*): BM1 OC1 SC2 PS2′ IL2 LR3 UR4 RR2 CC3 CPD2 CPR2 PLD1 PLG1 VG1 PAD1 PAG3 FG1.

Achatinoidea: Subulinidae (Figs. 341–352): A few genera from the European and North American Paleocene are assigned to the Subulinidae (Zilch, 1959–1960). The family is now pantropical, and includes the primarily circum-Mediterranean genus *Rumina.*

The Subulinidae are not carnivorous (BM1). An oesophageal crop occurs in only one of the four genera dissected (OC1, OC2). The gastric crop is inflated in its median portion (SC2, except in *Bocageia,* in which it is dedifferentiated: SC2′) and separated from the gastric pouch by a constriction (PS2′). The intestine is rather short (IL1, IL2). The kidney varies in length (LR1, LR2, LR3) and is generally differentiated internally into two distinct regions (RR1). The ureteric tube is closed as far as the pneumostome (UR4). The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium in length or long (CPD1, CPD2), the right one being longer than the left (CPR3, CPR4). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is either on the right side or in the middle (VG1, VG2). The right parietal ganglion touches and seems fused with the visceral ganglion in *Bocageia* and *Pseudoglessula* (PAD2, FG2); it is close to the right pleural ganglion and separated from the visceral ganglion in *Rumina* (PAD1, FG1).

Character states of the CCA: BM1 OC1 SC2 PS2′ IL1 LR1 UR4 RR1 CC3 CPD1 CPR3 PLD1 PLG1 VG1 PAD1 PAG3 FG1.

Achatinoidea: Achatinidae (Figs. 353–355): The Recent Achatinidae occur in tropical Africa only, and none is earlier than the Pleistocene (Zilch, 1959–1960). The Madagascan genus *Leucotaenius* belongs to the Acavidae (Mead, 1986). The Achatinidae are phenetically close to helicoids (Text-figs. 19, 20), but this might be the effect of their large size. I think that the Achatinidae might be simply giant subulinids, but the classification of the latter is so confused that I am unable to discuss the monophyly of the achatinids with one of the groups probably lumped together in the subulinids.

The sole species here dissected is distinct from the subulinids only in apomorphic character states that might result from large size: the oesophageal crop is very large (OC3), and the visceral chain is compact (PAD2, PAG4).

Character states of the CCA (= character states of *Achatina fulica*): BM1 OC3 SC2 PS2′ IL1 LR1 UR4 RR2 CC3 CPD2 CPR3 PLD1 PLG1 VG2 PAD2 PAG4 FG1.

Achatinoidea: Streptaxidae (Figs. 394–398): The Recent Streptaxidae are tropical African, South American, Indian and Oriental. A few Upper Cretaceous and Paleocene European genera have been assigned to the Streptaxidae (*Strophostomella, Lychnopsis, Enneopsis, Anastomopsis;* Zilch, 1959–1960); but I do not understand which characters other than size distinguish them from the Anadromidae, which occur in the same formations. The Recent Canarian genus *Gibbulinella* occurs in the south European Upper Cretaceous. Representatives of the genus *Rillya,* which is very similar to the Recent genus *Edentulina* in shell morphology, are known from the Paleocene, and the genus *Paracraticula,* which looks like a Recent enneine, occurs in the European Eocene. *Brasilennea* has been described from the Brasilian Miocene (Zilch, 1959–1960).

The Streptaxidae are phenetically close to the other carnivorous families, as in classical classifications (Zilch, 1959–1960; text-figs. 19, 20).

The buccal mass is very long, in association with carnivory (BM2). *Edentulina* differs from the other genera dissected in its possession of a large oesophageal crop (OC3, OC1). The gastric crop is cylindrical (SC1). The gastric pouch might be dedifferentiated (PS1, PS2), and the intestine is short, as a function of carnivory (IL2). The kidney is very short and internally homogeneous in morphology (LR4, RR2). The ureteric tube is closed as far as the pneumostome (UR4). The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium and subequal in length (CPD2, CPR2). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is median (VG2), in contact with both the parietal ganglia, from which it is, however, distinct (PAD2, PAG4, FG1). The pleuro-parietal connectives are longer than in any other family, as described above (carnivory).

Character states of the CCA: BM2 OC1 SC1 PS1 IL2 LR4 UR4 RR2 CC3 CPD2 CPR2 PLD1 PLG1 VG2 PAD2 PAG3 FG1.

This CCA differs from that of the ferussacids only in lesser differentiation of the gastric pouch, which may be due to carnivory, and in a shorter kidney; but the relatively greater length of the kidney in ferussaciids might be related to lung roof shortening.

Achatinoidea: Oleacinidae (+ Spiraxidae + Testacellidae) (Figs. 357, 361–374): The oleacinids range from the Eocene in Europe, and from the Miocene in Florida (Zilch, 1959–1960) to the Recent. The Recent species are South European, North African, Central American and Caribbean.

The Testacellinae are here included in the Oleacinidae, rather than recognized as a distinct family. This idea is not new (Watson, 1915), and reflects the refusal to base family-level divisions on autapomorphies related to limacization solely: the remarkable anatomical description of *Testacella* by Lacaze-Duthiers (1887) indicates that this genus might be derived easily from an ancestor similar to *Strebelia* (Figs. 372–374), except for internal kidney morphology.

Baker (1962) removed the genera *Euglandina, Spiraxis* and *Streptostyla* from the Oleacinidae to form the family Spiraxidae, which he considers close to the Sagdidae and Achatinidae (*v. supra;* Boss, 1982). This position is unacceptable. *Varicella* (Oleacinidae *sensu* Baker) is more similar to *Euglandina* and *Spiraxis* than to any other genus dissected here; furthermore the crop is anteriorly extended over the oesophagus as a rostrum in these three genera, not as in any other genus dissected but therhytidid *Priodiscus (v. infra).* Use of this character as a synapomorphy would produce a division different from that adopted by Baker: the Neotropical *Varicella, Spiraxis* and *Euglandina* (+ *Streptostyla?* + *Priodiscus??*) would form the sister group of the Neotropical and west Mediterranean group including *Poiretia, Strebelia* and *Testacella.* On the other hand, all the Neotropical genera dissected have a similar internal renal morphology, characterized by the absence of lamellae on the palatal surface of the kidney, as in ferussaciids. The west Mediterranean *Poiretia* and *Testacella* have lamellae on both the palatal and pulmonary surfaces of the kidney. The use of this character as a synapomorphy would lead again to a division different from that adopted by Baker.

All the Oleacinidae are carnivorous (BM2). *Euglandina, Varicella* and *Spiraxis* lack an oesophageal crop, but their gastric crop extends far forward as a rostrum. In *Poiretia,* the oesophagus is inflated and the gastric crop is not large. The morphology in the slugs *Strebelia* and *Testacella* might be derived from such an arrangement. The gastric pouch might be dedifferentiated (PS1, PS2; carnivory). The intestine might be very short (IL1, IL3), in relation to carnivory associated either with limacization (*Strebelia*), or with very small size (*Spiraxis*). The kidney is either short (LR2) and equilaterally triangular, or very short (LR4) and transversely elongate (heterurethry). It is not differentiated internally (RR2). *Spiraxis futilis* has a ureteric groove along the rectum (UR3). In the other genera dissected the ureter is closed as far as the pneumostome (UR4). The cerebral commissure is short (CC3). The cerebro-pedal connectives vary in length (CPD1, CPD2, CPD3); they are either subequal, or the right one is longer than the left (CPR2, CPR3, CPR4). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is on the left side of the median plane (VG3), and seems either distinct from the parietal ganglia or fused with the right one (FG1, FG2). The position of the right parietal ganglion varies (PAD1, PAD2). The left parietal ganglion touches both the left pleural and visceral ganglion (PLG3, PLG4).

Character states of the CCA: BM2 OC1 SC1 PS1 IL1 LR2 UR3 RR2 CC3 CPD1 CPR2 PLD1 PLG1 VG3 PAD1 PAG3 FG1.

Endodontoidea: Charopidae (Figs. 153–174): The Charopidae are nearly restricted to the Southern Hemisphere, although a few members of the family occur in North America. Their diversity is maximal in the Pacific Islands, particularly New Caledonia and New Zealand, but less in Australia, South Africa, Madagascar and southernmost South America (Solem, 1982).

The Charopidae are close together in the phenetic classification of the species, with the exception of the slug *Ranfurlya* (Text-fig. 19). They are close to the Systrophiidae, Punctidae and Endodontidae in the phenetic classification of the families (Text-fig. 20).

The Charopidae are not carnivorous (BM1), and lack an oesophageal crop (OC1). The anterior portion of the gastric crop is inflated, narrowing toward the gastric pouch (SC3), except in *Stephanoda,* in which the gastric crop widens toward the stomach as in the Discidae (SC2′). The gastric pouch is differentiated in most species dissected (PS1). The intestine is short (IL2). The kidney is short to very short (LR2 to LR4), and usually differentiated internally into two distinct regions (RR1). The ureteric tube is generally closed as far as the pneumostome (UR4), except in a few undescribed Australian genera (UR2; Solem, pers. comm.). The length of the cerebral commissure is medium to short (CC2, CC3). The cerebro-pedal connectives are medium in length (CPD2), except in the slug *Ranfurlya,* in which they are shorter (CPD3, limacization). The right pleural ganglion is closer to the right cerebral ganglion than to the pedal ganglion (PLD2, except in *Ranfurlya*), whereas the left pleural ganglion is nearer the left pedal ganglion (PLG1). The visceral ganglion is on the right side (VG1). The parietal ganglia are closer to the pleural ganglia than to the visceral ganglion (PAD1, PAG1), except in *Ranfurlya* (PAD2, limacization) and in *Mystivagor* (PAG2, elongate shape).

Character states of the CCA: BM1 OC1 SC3 PS1 IL2 LR2 UR2 RR1 CC2 CPD2 CPR1 PLD2 PLG1 VG1 PAD1 PAG1 FG1.

Endodontoidea: Punctidae (Figs. 175–183, 216): The genus *Punctum,* which is principally Palearctic, south and east African in distribution, occurs in the European Oligocene (Zilch, 1959–1960). Most Recent genera occur in New Zealand, the Pacific Islands, Australia, South Africa and South America (Solem, 1982). The Australian semislug *Cystopelta* is here placed among the Punctidae because it is similar to slugs belonging to the Endodontoidea *sensu* Solem, and to the athoracophorid slugs here considered endodontoids as well as to the Punctidae in its radular characters (Solem, pers. comm.).

The Punctidae are not carnivorous (BM1), and lack an oesophageal crop (OC1). The anterior portion of the gastric crop is inflated (SC3), except in *Cystopelta,* in which the cylindrical shape of the organ might result from limacization. The gastric pouch is differentiated (PS1), and the intestine is short (IL2). The kidney is short (LR3) and internally differentiated into two distinct regions (RR1). The ureteric tube is closed as far as the pneumostome (UR4). The cerebral commissure is short (CC3). The cerebro-pedal connectives are medium in length (CPD2; short in *Cystopelta:* limacization?), the right one being longer than the left (CPR3, except in *Cystopelta*). The right pleural ganglion is close to the right cerebral ganglion (PLD2), whereas the left pleural ganglion is closer to the left pedal ganglion (PLG1) (compaction occurs in *Cystopelta*). The visceral ganglion is on the right side of the median plane, and seems fused with the right parietal ganglion (VG1, FG2). The left parietal ganglion is closer to the left pleural than to the visceral ganglion (PAG1).

Character states of the CCA: BM1 OC1 SC3 PS1 IL2 LR3 UR4 RR1 CPD2 CPR3 PLD2 PLG1 VG1 PAD2 PAG1 FG2.

Endodontoidea: Athoracophoridae (Figs. 218–220): The Athoracophoridae are all slugs and are Australasian. Phenetically, the non-athoracophorid species closest to the Athoracophoridae is the Australian endodontoid slug *Cystopelta* (Text-fig. 19). At the familial level, the Athoracophoridae are more similar to the Arionidae (Philomycinae included) and Vitrinidae than to any other family (Text-fig. 20).

The diet is not carnivory (BM1), and the crop is cylindrical (SC1). The gastric pouch is reduced (PS2). The intestine is very long, as a function of advanced limacization (IL2′; Tillier, 1984a). The kidney is compact (LR5) and filled with anastomose lamellae (RR2). The ureteric tube is closed to the pneumostome, and forms numerous convolutions (Plate, 1898; Tillier, 1983). The cerebral commissure is short (CC3). Connectives could not be distinguished owing to compaction of the central nervous system (CPD3, PLD3, PLG3); the asymmetry in the arrangement of the parietal and pleural ganglia, which seem fused (Fig. 220), suggests that in the athoracophorid ancestors the left pleural ganglion was close to the left pedal ganglion, and the right pleural ganglion was close to the right cerebral ganglion (PLD2, PLG1). The visceral ganglion lies to the right of the median plane (VG1), and seems fused with both parietal ganglia (PAD2, PAG4, FG3).

Character states of the CCA: BM1 OC1 SC1 PS2 IL2′ LR5 UR4 RR2 CC3 CPD3 CPR2 PLD2 PLG1 VG1 PAD2 PAG4 FG3.

Endodontoidea: Endodontidae (Figs. 147–152): The family Endodontidae is endemic to the Central Pacific Islands (Solem, 1976). Both species here dissected are close to the Charopidae, Punctidae and Systrophiidae in the phenetic classifications (Text-figs. 19, 20).

Genital and radular characters of this family have been discussed by Solem (1976). In characters used here, the Endodontidae differ from the Charopidae in the dedifferentiation of their gastric pouch (PS2), in the position of the left pleural ganglion close to the cerebral ganglion (PLG2), and in a ureteric tube not closed farther than kidney-rectum angle (UR2, found also in a few Australian Charopidae).

Character states of the CCA: BM1 OC1 SC3 PS2 IL2 LR3 UR2 RR1 CC2 CPD2 CPR1 PLD2 PLG2 VG1 PAD1 PAG1 FG2.

The CCA of the Endodontidae has either the same character states as the CCA of the Charopidae, or more apomorphic states. Consequently the CCA of the Charopidae is a CCA of the Endodontidae, but the converse is not true. This finding contradicts the opinion of Solem (1982), who estimates that the Endodontidae are closer to the common ancestor of both families than are the Charopidae, or even represent the stem group of the Endodontoidea.

Endodontoidea: Systrophiidae (Figs. 399–405): The Systrophiidae are Neotropical, but do not occur in the Greater Antilles and in Central America. They share a synapomorphy, contiguity between both pleural ganglia with the cerebral ganglia associated with the grouping of the right pleural, right parietal and visceral ganglia beneath the right cerebral ganglion (exaptation or adaptation to carnivory). In the phenetic classification of the families they are close to the Charopidae, Punctidae, Endodontidae and Euconulidae (Text-fig. 20).

The Systrophiidae are carnivorous, but their buccal mass is not always elongate (BM1, BM2). They do not have an oesophageal crop (OC1). The gastric crop becomes narrower toward the gastric pouch (SC3), which might be dedifferentiated (PS2, carnivory). In *Systrophia* the anterior duct of the digestive gland opens into the gastric crop farther forward than in any other stylommatophoran dissected (Figs. 399, 405), with the exception of *Ventridens* (Gastrodontinae, Fig. 269), which has the same arrangement. The intestine is short (IL2). The kidney is relatively long (LR1) in all species dissected, *Systrophia eudiscus* excepted (LR2); this relatively great length may result from shortening of the visceral mass and lung. The ureteric tube is only partly closed in *Systrophia eudiscus* (UR2), and closed as far as the pneumostome in the other species dissected. In the latter, it runs across the pneumostome along the lung roof and opens on the side of the pneumostome opposite the anus (Tillier, 1980). There are two regions inside the kidney pouch (RR1); a thick internal lamella runs along the rectal border of this pouch. The cerebral commissure is short (CC3), the lateral connectives are medium and subequal in length (CPD2, CPR2), and the visceral chain has the peculiar arrangement described above.

Character states of the CCA: BM1 OC1 SC3 PS1 IL2 LR2 UR2 RR1 CC3 CPD2 CPR2 PLD2 PLG2 VG1 PAD2 PAG1 FG2.

Clausilioidea: Clausiliidae (Figs. 505–520): Recent Clausiliidae occur from Indonesia to Europe, in the Greater Antilles and in northern South America. The subfamily Neniinae includes the Neotropical taxa, as well as two doubtfully attributed Oriental genera (Zilch, 1959–1960). The subfamily Phaedusiinae occurs in the European Danian. Zilch (1959–1960) considers the European Eocene and Oligocene Filholiidae related to the Clausiliidae. The family Megaspiridae, which includes a few European Eocene taxa and Recent genera in Brazil, New Guinea and Queensland, has been interpreted by Pilsbry (1904) as related to this group.

In the phenetic classifications of the species (Text-fig. 19) and of the families (Text-fig. 20), the Clausiliidae are close to the Urocoptidae on the one hand and to the Ferussaciidae and Succineidae on the other.

The diet of the Clausiliidae is never carnivory (BM1), and no oesophageal crop has been seen (OC1). The median portion of the gastric crop is inflated (SC2), and the crop is separated from the well-differentiated gastric pouch by a constriction (PS2′). The intestine is short (IL2). The kidney is very short (LR3, LR4), and is not differentiated internally (RR2). There is no ureteric tube (UR1). The cerebral commissure is very long (CC1). The cerebro-pedal connectives are medium to short in length (CPD2, CPD3), the right one being shorter than the left (CPR1, CPR2; the observed asymmetry is actually reversed because the Clausiliidae are sinistral). The pleural ganglia are usually closer to the pedal ganglia than to the cerebral ganglia (PLD1, PLG1). The visceral ganglion is either on the right side, or median (VG1, VG2) and does not seem fused with either of the parietal ganglia (FG1). The parietal ganglia are closer to the visceral than to the pleural ganglia, and may touch the former (PAD1, PAD2, PAG2, PAG3).

Character states of the CCA: BM1 OC1

SC2 PS2′ IL2 LR3 UR1 RR2 CC1 CPD2 CPR1 PLD1 PLG1 VG1 PAD1 PAG2 FG1.

Clausilioidea: Cerionidae (Figs. 521–527): The Cerionidae are endemic to the Antillean region, from Florida to the Venezuelan coast. The earliest genus is *Eostrophia*, from the Miocene of Florida (Zilch, 1959–1960).

Their proximity in the phenetic classification of species to *Urocoptis* (Text-fig. 19) is more representative of their obvious similarity to the Urocoptidae than is their position in the phenetic classification of families (Text-fig. 20) among the Orthurethra, which reflects the great length of the kidney in one of the species dissected.

Dissection of a series of *Cerion* belonging to several species recognized by Gould and Woodruff (*C. casablancae, C. glans, C. rubicundum, C. agassizi, C. copium;* Woodruff, 1978; Chung, 1979) shows that intraspecific variation in proportions of the lengths of the organ systems is more marked here than in any other group studied. This variability, together with the similarity of cerionids to urocoptids, leads me to consider the great length of the kidney seen in some species of *Cerion* secondary, not plesiomorphic.

The cerionids are not carnivorous (BM1), and lack an oesophageal crop (OC1). The gastric crop is cylindrical (SC1). The gastric pouch is differentiated (PS1) and might be separated from the gastric crop by a constriction (PS2′). The intestine is medium in length (IL1). The kidney is short (LR3, LR4), sometimes secondarily longer (LR2, LR1), and not differentiated internally (RR2). There is no ureteric tube (UR1). The cerebro-pedal connectives and the cerebral commissure are medium in length (CC2). The left cerebro-pedal connective is longer than the right one (CPR3). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion is median (VG2), and in contact with both parietal ganglia (PAD1, PAG3).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR3 UR1 RR2 CC2 CPD2 CPR3 PLD1 PLG1 VG2 PAD1 PAG3 FG1.

Clausilioidea: Urocoptidae (Figs. 528–535): Recent Urocoptidae are endemic to Central America and to the Antillean region. The Recent Mexican genus *Holospira* also occurs in the North American Paleocene (Zilch, 1959–1960). The Urocoptidae are close to the Clausiliidae in the phenetic classification of the families (Text-fig. 20).

Urocoptids are not carnivorous (BM1), and they lack an oesophageal crop (OC1). The median portion of the gastric crop is inflated (SC2). The morphology of the gastric pouch is variable (PS1, PS2, PS2′). The intestine is short (IL2). The kidney is short (LR3, LR4), and not differentiated internally (RR2). The length of the ureteric tube is very variable: *Macroceramus* has no ureteric tube (UR1); the ureteric tube reaches the recto-visceral angle of the kidney in *Urocoptis* (UR2), and nearly reaches the pneumostome region in *Berendtia* (UR3). The cerebral commissure is short (CC3). The cerebro-pedal connectives are long (CPD1) and subequal in length (CPR2). The visceral chain has the same arrangement seen in the Cerionidae (PLD1, PLG1, VG2, PAG3), but is more compact through apparent fusion of the left parietal and visceral ganglia (FG2′) and contact of the right parietal with the right pleural ganglia (PAD2).

Character states of the CCA: BM1 OC1 SC2 PS1 IL2 LR3 UR1 RR2 CC3 CPD1 CPR2 PLD1 PLG1 VG2 PAD2 PAG3 FG2′.

Clausilioidea: Bulimulidae (Figs. 536–555): The Bulimulidae are Neotropical and Australasian. The oldest known representative is *Paleobulimulus*, from the Patagonian Eocene (Parodiz, 1969).

In the phenetic classifications of both species and families, the Bulimulidae are close to helicoids (Text-figs. 19, 20).

The Bulimulidae are not carnivorous (BM1) and have an oesophageal crop (OC2, OC3). The gastric crop is either cylindrical (SC1), or inflated in its median portion (SC2). The gastric pouch is variable in morphology (PS1, PS2, PS2′) and frequently divided internally into two chambers by a fold in the plane of separation of the crop and intestine. The intestine is medium to long in length (IL1, IL2′). The kidney is short (LR3), but may be secondarily longer in taxa with a shortened visceral mass and lung (*Simpulopsis, Pellicula*), and is not differentiated internally (RR2). The ureteric tube reaches a point between the upper extremity of the lung and the pneumostome (UR3, UR4). The cerebral commissure is variable in length (CC1, CC2, CC3). The cerebro-pedal connectives are medium to long and subequal in length (CPD1, CPD2, CPR2). The pleural ganglia are close to the pedal ganglia (PLG1, PLD1). The visceral ganglion is on the left side of the median plane (VG3) and seems fused with the left parietal ganglion (FG2′) or with both parietal ganglia (FG3). The visceral chain is compact (PAD2, PAG3, PAG4).

Character states of the CCA: BM1 OC2 SC1 PS1 IL1 LR3 UR3 RR2 CC1 CPD1 CPR2 PLD1 PLG1 VG3 PAD2 PAG3 FG2′.

Acavoidea: Oreohelicidae (+ Ammonitellidae) (Figs. 492–504): The Ammonitellidae *auctt.* are here considered to belong to the Oreohelicidae, because the Oreohelicidae *auctt.* differ from them only in more apomorphic character states, and because both groups are endemic to North America. The two groups are close together and close to the Haplotrematidae in the phenetic classification of the families (Text-fig. 20). The species dissected are close to helicoids in the phenetic classification of the species (Text-fig. 19).

The Ammonitellinae (Figs. 497–504) consists of three Recent genera and is endemic to North America, where at least one species occurred in the Upper Cretaceous (Solem, *in litt.*). These animals are not carnivorous (BM1), and they lack an oesophageal crop (OC1). The gastric crop is cylindrical, or inflated in its median portion (SC1, SC2). The gastric pouch is differentiated and is separated from the gastric crop by a constriction in *Glyptostoma* (PS1, PS2′). The intestine is medium to long in length (IL1, IL2′). The kidney is short (LR3, LR4), and is not differentiated internally (RR2). The ureteric tube is not closed farther than the recto-visceral extremity of the kidney (UR2). The cerebral commissure varies in length (CC1, CC3). The cerebro-pedal connectives are long and, when they are unequal in length, the right one is the longer (CPD1, CPR1, CPR2). The pleural ganglia are close to the pedal ganglia in *Glyptostoma* (PLD1, PLG1), but close to the cerebral ganglia in *Ammonitella* (PLD2, PLG2). The visceral ganglion is on the right side of the median plane (VG1), and seems fused with the right parietal ganglion in *Ammonitella* only (FG1, FG2). The left parietal ganglion touches the visceral ganglion (PAG3).

The Oreohelicinae (Figs. 492–496), now endemic to western North America, occur in the Upper Cretaceous of the same region (Zilch, 1959–1960). The only species dissected, *Oreohelix barbata,* differs from the Ammonitellinae dissected in its shorter ureteric tube, the length and asymmetry of its cerebro-pedal connectives (CPD3, CPR3), and the asymmetric arrangement of its pleural ganglia (PLD2, PLG1).

Character states of the CCA: BM1 OC1 SC1 PS1 IL1 LR3 UR2 RR2 CC1 CPD3 CPR3 PLD2 PLG1 VG1 PAD2 PAG3 FG1.

Acavoidea: Corillidae (Figs. 470–491): The family Corillidae, unknown as fossils, includes only five genera: *Sculptaria* in South Africa, *Corilla* in Sri Lanka and southern India, *Plectopylis* in Indochina, *Amphicoelina* in China and *Craterodiscus* in Australia. *Craterodiscus* is here removed from the Camaenidae because the morphology of its pulmonary complex is similar to that of *Sculptaria* and *Plectopylis.* Furthermore, it lacks an oesophageal crop, as do all corillids; all dissected camaenids have such a crop. A ureteric tube reaching the pneumostome cannot be used to exclude *Craterodiscus* from the Corillidae, because several species of *Plectopylis* exhibit the same character state (Solem, 1966a; Solem & Tillier, unpublished observations). On the other hand, *Craterodiscus* differs from all the other Corillidae dissected in the extreme shortness of its intestine; however, this character state is not seen in any camaenid, and might be related to the very small size of *Craterodiscus.*

In the phenetic classification of the families, the Corillidae are close to the groups that include the Urocoptidae, Clausiliidae and Rhytididae (Text-fig. 20).

The buccal mass is spheroidal (BM1), and an oesophageal crop is absent (OC1). The gastric crop is cylindrical or inflated in its anterior portion (SC1, SC3). The gastric pouch varies in shape and degree of differentiation (PS1: medium size; PS2′: large size; PS2: small size). The intestine is very long (IL2′), except in *Craterodiscus* (IL2: very small size). The kidney is very short (LR4), and is not differentiated internally (RR2). There is usually no ureteric tube (UR1), but a few species have a ureteric tube reaching the pneumostome (UR4). The cerebral commissure is variable in length (CC1, CC2, CC3). The cerebro-pedal connectives are medium to long and subequal in length (CPD1, CPD2, CPR2). The right pleural ganglion is close to the right cerebral ganglion (PLD2), except in *Corilla,* in which it is closer to the right pedal ganglion (PLD1; large size?). The left pleural ganglion is close to the pedal ganglion in all species dissected (PLG1). The visceral ganglion is either median (VG2) or on the left side (VG3). Apparent fusion of the visceral and parietal ganglia does not occur (FG1) except in *Craterodiscus,* in which the three ganglia form a single mass (FG3). Whenever the visceral chain is not compact, the left parietal ganglion is closer to the left pleural than to the visceral ganglion (PAG1), and the right parietal ganglion is distinct from the visceral ganglion (PAD1).

Character states of the CCA: BM1 OC1 SC1 PS1 IL2′ LR3 UR1 RR2 CC1 CPD1 CPR2 PLD1 PLG1 VG2 PAD1 PAG1 FG1.

Acavoidea: Acavidae (Figs. 406–469): The Acavidae occur in South Africa, South America, Madagascar, the Seychelles, Sri Lanka and Australia. The living genera *Strophocheilus* and *Dorcasia* range respectively in South America and in South Africa from the Paleocene to the Recent. I reject the arrangement adopted by Boss (1982), who divides the Acavidae into several families placed in different superfamilies and suborders. Although it is likely that the Acavidae include several monophyletic groups, I do not know of any synapomorphy which might define these groups and unite some of them with other families. The Acavidae are united by overall similarity and by their general trend of shortening of the visceral mass with deformation of the kidney, as described above. *Solaropsis* might be included in the family on this basis, but in this case *Labyrinthus* and *Isomeria* should be included too (*v. supra*).

Phenetically the Acavidae are close to the groups that include the Helicoidea, Bulimulidae and Achatinidae (Text-fig. 20).

The Acavidae are generally not carnivorous and have a spheroidal buccal mass (BM1), with the exception of the Seychellian *Stylodon* and South American *Macrocyclis* (BM2). An oesophageal crop might be present and very large (OC1, OC2, OC3, OC4). The gastric crop varies in shape (SC1, SC2, SC2′). The gastric pouch is differentiated (PS1, PS2′). The intestine is very long (IL2′), except in the semislug *Pandofella* (IL1). The kidney varies in length in relation to lung shortening, as shown above (LR1, LR2, LR3, LR4). The plesiomorphic state is probably the state related to minimum deformation in the arrangement of the lung roof and kidney, i.e. LR3 (kidney short). A ureteric tube might be absent or present, although never reaching the pneumostome (UR1, UR2, UR3), and the kidney might be divided internally into two distinct regions (RR1, RR2). The cerebral commissure is medium to short in length (CC2, CC3). The cerebro-pedal connectives are generally long, but can be very short (CPD1, CPD2, CPD3). When they are unequal, the right one is shorter than the left (CPR2, CPR3, CPR4). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion varies in position (VG1, VG2, VG3), and is generally distinct from the parietal ganglia (FG1); apparent fusion occurs with the right parietal ganglion, if present (FG2). The visceral chain is generally compact; however, *Caryodes* has a very long visceral chain despite its large size, and its parietal ganglia touch its visceral ganglion (PAD1, PAG3).

Character states of the CCA: BM1 OC1 SC1 PS1 IL2′ LR3 UR1 RR1 CC2 CPD1 CPR2 PLD1 PLG1 VG1 PAD1 PAG3 FG1.

Acavoidea: Rhytididae (+ Chlamydephoridae) (Figs. 375–393): According to their current definition, adopted by Zilch (1959–1960), the Rhytididae occur in South Africa, the Seychelles and the Australasian region. The Rhytididae are phenetically close to the Oleacinidae, Streptaxidae (carnivory) and Corillidae.

Some Acavidae being carnivorous (*Stylodon, Macrocyclis*), it is difficult to define a limit between them and the Rhytididae. The Rhytididae might be defined by a synapomorphy, the presence of loops of the ureteric tube between the renal pore and the rectal side of the kidney: such loops are either between the pericardium and the kidney (*Nata, Rhytida;* incipient in *Ouagapia* and *Schizoglossa*), or along the pulmonary vein distal to the renal pore (*Diplomphalus*). If accepted, this solution would exclude *Natalina* (Watson, 1934) and *Priodiscus* from the Rhytididae. If transferring *Natalina* to the Acavidae is not particularly problematic, such is not the case with *Priodiscus,* which has several features that might indicate other relationships. First, the nervous system has the arrangement found elsewhere only in the Streptaxidae, i.e. very long parieto-pleural connectives (compare Figs. 376, 396). Second, the anterior portion of the gastric crop is developed as a rostrum, occurring elsewhere only in some American Oleacinidae (*v. supra*). Third, its kidney has internal lamellae only on its pulmonary surface, as in American Oleacinidae and some Corillidae. Fourth, its shell (Zilch, 1959–1960, Fig. 1921) reminds one of the shells of the Rhytididae only because it is rather flat, but does not resemble more closely the shells of the

Streptaxidae or of the Oleacinidae. Fifth, in terms of overall similarity, *Priodiscus* resembles more closely *Craterodiscus* (Corillidae) than it does any member of the three carnivorous families (Text-fig. 19).

My knowledge of the genital anatomy in these families is not sufficient for me to judge the affinities of *Priodiscus*, of which the genital apparatus is shown in Fig. 379.

The case of the Chlamydephorinae is far simpler, and I do not hesitate to include *Chlamydephorus* in the Rhytididae because the New Zealand rhytidid slug *Schizoglossa* is intermediate in morphology between rhytidid snails and these very advanced slugs (Watson, 1915; Figs. 392,393).

These animals are carnivorous, and their buccal mass is always cylindrical (BM2). In *Nata*, *Schizoglossa* and *Chlamydephorus* (OC2) the anterior portion of the oesophagus instead of the median portion is inflated to form the oesophageal crop. The other genera lack an oesophageal crop (OC1). The gastric crop either is cylindrical (SC1), or becomes narrower toward the stomach (SC3). The gastric pouch is dedifferentiated (PS2), except in *Priodiscus* (PS1). The intestine is usually very long (IL2′), except in the slug *Schizoglossa* (IL2, limacization), and in *Priodiscus*, in which its very short length might be related to the association of carnivory with small size (IL3). The kidney is short (LR3), except in taxa having the visceral mass and lung secondarily shortened (LR2, LR1); the first branch of the pulmonary vein is particularly developed in *Rhytida*, which has such a short visceral mass and lung, as in the Acavidae. The kidney is not differentiated internally (RR2). The ureteric tube is not closed farther than the upper extremity of the kidney in three genera of five dissected. It is closed as far as the pneumostome in the slug *Schizoglossa* (limacization), and in *Priodiscus*. The cerebral commissure is short (CC3). The cerebro-pedal connectives are subequal and vary in length (CPR2, CPD1, CPD2, CPD3). The pleural ganglia are close to the pedal ganglia (PLD1, PLG1). The visceral ganglion lies in the median plane (VG2) or, in *Priodiscus*, on the left side (VG3). The parietal and visceral ganglia form a single mass separated from the pleural ganglia by distinct connectives, as in the acavid *Caryodes* and in the Streptaxidae (PAD1, PAG2). However, except in *Priodiscus*, the parieto-pleural connectives are much shorter than those in the Streptaxidae. The three ganglia might seem fused together (FG1, FG3).

Character states of the CCA (excluding *Priodiscus* because of its problematic affinities): BM2 OC1 SC1 PS2 IL2′ LR3 UR2 RR2 CC3 CPD1 CPR2 PLD1 PLG1 VG2 PAD1 PAG3 FG1.

PHYLOGENY AND CLASSIFICATION

Principles and methods of classification of Stylommatophora

Phenetic nature of classical classifications: Although not identical to any current classification, the phenetic classification of the stylommatophoran families presented in Text-fig. 20 is familiar to a systematist of land snails. Comparison with Appendix A, in which the sequence of families follows Zilch's classification (1959–1960), shows that the members of the Holopoda, Aulacopoda and Orthurethra cluster together in a somewhat similar order. Most families of which the position seems aberrant in Text-fig. 20 belong either to the Mesurethra, as might be expected when not overweighting the absence of a ureteric tube, or to the never-defined trash-can group of the Holopodopes formed by Baker by lumping together those families not clearly belonging to the Aulacopoda, Holopoda or Orthurethra. Although I have not done so, I have little doubt that any classification produced by the Pilsbry-Baker school could be obtained easily by the method used to obtain Text-fig. 20 by weighting various characters. The similarity of current classifications to this phenetic classification might be surprising, inasmuch as the latter was built with 31 characters of which only one, the degree of closure of a ureteric tube, has been explicitely used before.

On the other hand, it seems impossible to formulate any clear, precise diagnosis of the suprafamilial groups proposed by the Pilsbry-Baker school. When by chance a character might seem diagnostic, its mention should include a list of exceptions. The relatively great length and the internal structure of the orthurethran kidney, without any mention of the absence of a ureteric tube which is not general within the group, constitutes an exception, but its use was unfortunately abandoned after Pilbry (1900a). The synthetic work of Boss (1982) is illustrative of this situation, in which it is impossible to find the position of a given snail or slug by using his diagnoses, of which each element is repeated in several diagnoses. The reason for this apparent confusion lies not in the quality of the work, but in the empiricism of earlier authors who never defined the rationale upon which they based their classifications and never defined clearly the suprafamilial groups that they proposed (e.g. Baker, 1955; Solem, 1978).

It may be deduced from these two remarks that first, the classifications elaborated by the Pilsbry-Baker school are basically phenetic, although *originally* based on outgroup comparison (Pilsbry, 1896, 1900a) and secondly, the phenetic nature of his classification was not clearly understood and controlled by Baker himself, who implicitly used characters that he had seen but never mentioned and possibly never explicitly considered. This approach resulted in a classification that is reasonably stable and resistant to the inclusion of new taxa, but which hardly can be understood and handled without personal experience in land snail anatomy.

The principle upon which current classifications are built being identified, it should of course be possible to improve the method and, by studying more taxa and more characters than was done here, to obtain a classification that would be reasonably stable whatever the phenetic distance used. Analysis of the nodes of such a tree would allow the explicit identification of the characters that discriminate the groups in a more satisfying manner than presently. This way seems safe, but not very attractive: even without consideration of the arguments tending to show that a phylogenetic classification is more stable than a phenetic classification (Wiley, 1981), I prefer to try to build a phylogenetic classification of land snails that reflects as far as possible the evolutionary history of the group.

Principles of phylogenetic classification: Hypotheses about the characters useful for phylogenetic purposes, about the direction of evolution of these characters and about their ancestral states having been accepted in the preceding discussion, the phylogenetic relationships of the hypothetical common ancestors (CCA) of the various families can now be discussed. However, the members of only one group, the Orthurethra, share a synapomorphy *sensu stricto,* i.e. a seemingly uniquely derived character state, in kidney morphology; in later discussion, synapomorphy is used *sensu lato* for derived character states shared by members of a supposedly monophyletic group, but not necessarily unknown in other groups. This synapomorphy *s.s.* is confirmed by their morphological homogeneity, which appears even when characters that are not correlated in the other stylommatophoran groups are used (functionally independent characters?). Within the Orthurethra and among the other stylommatophoran groups, there is virtually no character state which can be used as a synapomorphy *sensu stricto:* nearly every apomorphic state occurring in two families also occurs elsewhere, without giving by itself any indication of common ancestry, and the various trees that can be constructed with the various characters are so incongruent that hypotheses about monophyly can hardly be proposed on such a basis. This result suggests that, at least at the morphological levels discussed here, parallel evolution is the rule rather than the exception, and illustrates Eldredge's (1979:170, fn) statement, "As a result of the relatively recent production of a plethora of cladograms, parallelism turns out to be a far more common evolutionary phenomenon than even most of its more ardent aficionados had thought." In theory the classical Hennigian method avoids the use of distance; in practice it reveals the generality of parallel evolution and, as discussed below, the need to minimize the length of the phylogenetic trees, not because the shortest tree is necessarily the best, but because nobody has yet found another solution.

A first approach to this problem was explored by the late Pierre Delattre (unpublished). In the data set, every object is represented by a sequence of indices as in the matrices commonly used in numerical phylogenetics. Each index represents a character of which the states are symbolized by values ranging from 1 (plesiomorphic) to n (apomorphic). An object having all its indices at most equal to those of another object, and having at least one index lower than the equivalent index of this other object is a possible ancestor of this other. It is therefore possible to reconstruct all the possible ancestors of any object, *as long as reversal is not allowed.* For example, an object denoted 121 has six possible ancestors, 111, 011, 001, 101, 100 and 000. It is then possible to construct the possible closest common ancestor (= CCA) of any pair of objects by taking the lowest value of each index found in both, and all the possible ancestors of this CCA are also common possible ancestors of this pair. For example, the objects noted 123 and 321 have 121 as CCA, and the six objects listed above are also possible common ancestors of this pair. All possible phyletic relationships in any data set can be determined in this way and, if the set is not too large, a network diagram can be constructed to show for discussion any possible path and eliminate most of the paths until a tree is obtained (if hybridization is not allowed).

A few attempts with real data showed that the number of possible relationships is lower than one might have feared, and that this method is convenient for small data sets. Unfortunately, even if most of the possible trees are eliminated the method cannot be applied directly here, where, with 50 taxa and 17 characters, the number of possible phyletic paths is too large to allow discussion of each. However, it can be applied to a data set corresponding to a tree of which the length has already been minimized.

Minimizing the length of a diagram of phylogenetic relationships is not necessarily parsimony, contrary to what many systematists seem to think: parsimony is reduction of the number of *ad hoc* hypotheses necessary to justify the choice of a given path, but not the reduction of the length of this path, which is minimization. The minimization of the length of phylogenetic trees is generally justified on the grounds that each independent appearance of an apomorphic state requires an *ad hoc* hypothesis; and that consequently, reducing the number of independent appearances of derived character states, equivalent to reducing the length of the tree, is parsimony (Wiley, 1981).

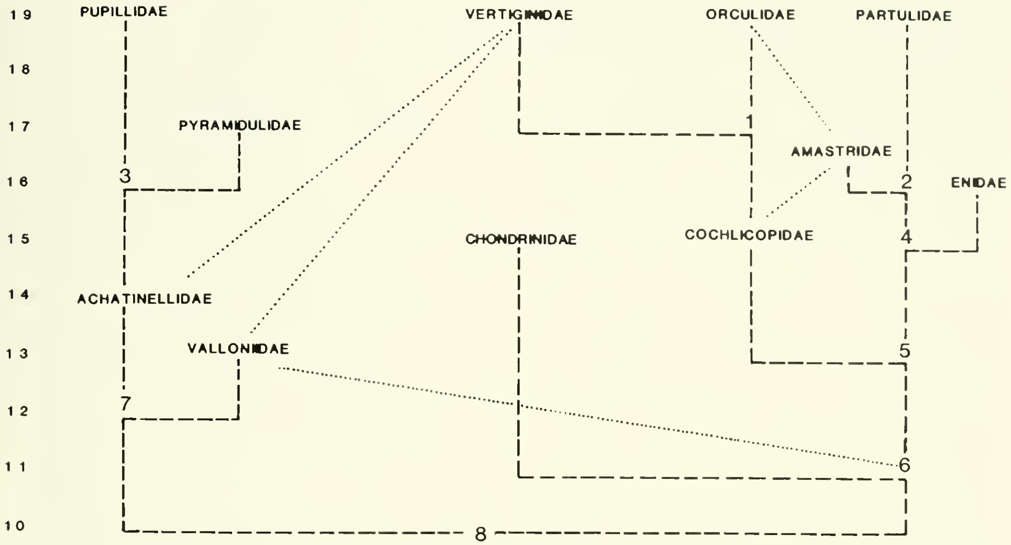
The problem raised by this interpretation is that the only coherent and available theory of evolution is the synthetic theory, which attributes the differences between taxa to a combination of chance and natural selection (adaptation), but does not establish any direct relationship between evolution and phylogeny (Tillier, 1986); it does not justify the minimization of the number of independent derivations of a given character state but, on the contrary, provides a single general *ad hoc* hypothesis that explains all convergences by adaptation and therefore justifies disregarding the number of independent derivations of a given character state in constructing a phylogenetic diagram. There is, therefore, a contradiction between the current theory of evolutionary mechanisms and the practice of numerous phylogenetic systematists, which perhaps has more to do with blindness than with parsimony: a contradiction can hardly be resolved by ignoring one of its terms.

Two attitudes seem to me consistent under such conditions. First, one can accept the synthetic theory only, and construct phylogenetic diagrams by using minimization. The resulting diagram represents a synthesis of chance and environmental conditions, but there is no reason to believe that it reflects the phylogenetic relationships unless a *complete* series of fossils is available (Utopia). The taxa constituted in this manner are ecological groups that are probably para- or polyphyletic; at least the theory does not provide any argument in favor of their monophyly. Secondly, one can introduce an *ad hoc* hypothesis that, without refuting the current results as to the mechanisms of microevolution, justifies minimization. I propose the following hypothesis: the closer the phylogenetic relationships of two taxa are (i.e., the greater the ratio of the number of their common ancestors and of the total number of their ancestors is), the greater the probability for the appearance of the same derived character states in the two taxa.

This postulate reminds one of Vavilov's law of homologous series in variation (1922). Cain (1982:393) asserts it at least at infrageneric level (". . . it is precisely in those stocks which are already closely allied that convergence is most likely to occur . . ."). As discussed by Gould (1983), Vavilov's law is not Darwinian, or at least not neo-Darwinian: in the fifth chapter of "Origin of Species", Darwin explicitly used analogous morphoclines as an argument for a common origin, and therefore implicitly considered their states as homoiologous as construed by Sneath and Sokal, 1973); furthermore, Vavilov's law does not allow innovation. The postulate presented here is no more neo-Darwinian, and supposes that all variations are not equiprobable, but that the members of every lineage vary within a well-defined potential for variation, which is modified to only a limited extent by each speciation event. Such an *ad hoc* hypothesis justifies the use of phenetic classifications in the search for phylogenetic relationships, and explains the general similarity of phenetic and phylogenetic classifications of the same group.

Method of phylogenetic classification: The method employed here consists in:

1. Construction of a short tree of phyletic relationships among the CCAs of the various families;



TEXT-FIG. 21. Network of possible phyletic relationships among orthurethran families. Indices of nodes, Appendix F. Numbers to the left correspond to sums of indices of nodes:
Possible ancestor-descendant relationships between nodes:
Achatinellidae: Vertiginidae, Pyramidulidae, Pupillidae, =3=.
Amastridae: Orculidae.
Cochlicopidae: Amastridae, Vertiginidae, Orculidae, =1=.
Valloniidae: Vertiginidae.
=1= : Vertiginidae, Orculidae.
=2= : Orculidae, Partulidae, Amastridae.
=3= : Pyramidulidae, Pupillidae.
=4= : Orculidae, Partulidae, Amastridae, Enidae, =2=.
=5= : Partulidae, Amastridae, Cochlicopidae, Vertiginidae, Orculidae, Enidae, =1=, =2=, =4=.
=6= : Partulidae, Amastridae, Cochlicopidae, Vertiginidae, Orculidae, Chondrinidae, Valloniidae, Enidae, =1=, =2=, =4=, =5=.
=7= : Achatinellidae, Pyramidulidae, Vertiginidae, Pupillidae, Valloniidae, =3=.

2. Determination of the other possible kinship relationships among the nodes without calculating additional nodes;

3. Choice of paths;

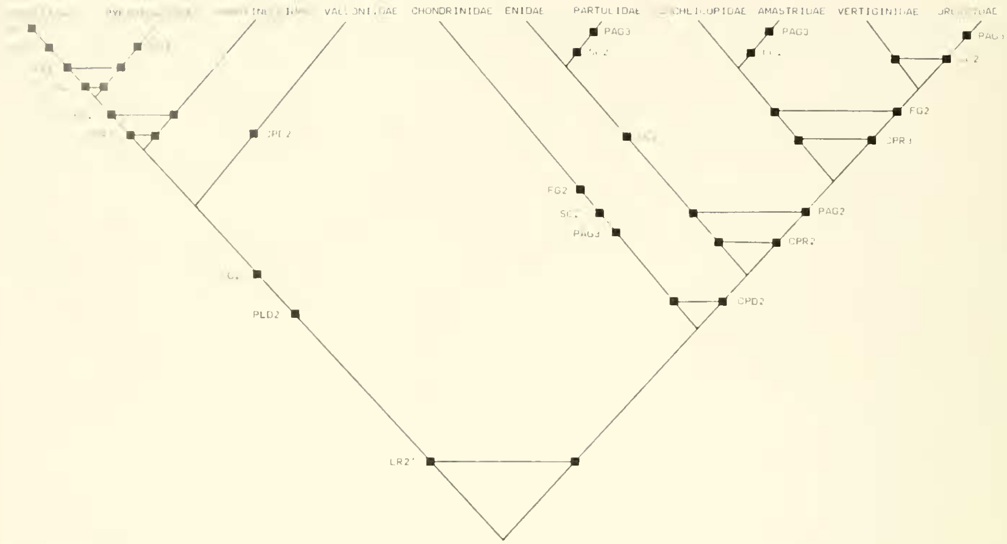
4. Possibly, return to step one using the CCAs of the various branches retained after step three as the data set; the necessity for this step results from the algorithm used, in which the stability of the nodes is less closer to the root of the tree;

5. Construction of a tree representing the phyletic relationships that have been retained.

Before the last step, some objects are in the position of ancestors: This point does not seem very important, because first, all the objects actually handled are abstractions; and second, the only really important point is the relative position of the actual taxa. The topological relationship of three points A, B, C is the same if the points are located along a line ABC or at the extremities of the branches of a tree (A(BC)) or ((AB)C), i.e. B is between A and C (the position of the root is here determined independently, because reversal is not allowed).

The data set is constituted by the CCAs of the various families, as defined above (Appendix F). Characters of which the plesiomorphic state is not an extremity of a morphocline, denoted 1, 2, 3 or 1, 2′, 3′ in Appendix F, were recoded in two columns: the plesiomorphic state was recoded 11; one part of the morphocline was coded 12, 13, etc., and the other part of the morphocline was coded 21, 31, etc. The distance is the Manhattan distance (Wiley, 1981).

Two algorithms have been tested (and the PENNY program of the PHYLIP package: *v. infra*). Only the one used further is here described in detail. The values of each index



TEXT-FIG. 22. Phylogenetic tree of the Orthurethra. Branches correspond to paths of Text-Fig. 21 that were retained.

were determined by outgroup comparison, and every CCA was defined by the lowest values of the indices in all members of the group of which the CCA was sought. The sequence of steps is:

1. Find the object of which the sum of the indices is the largest;
2. Find a second object such that the CCA of both objects is close to the first one;
3. When several objects fit the criteria of step two, choose the object such that the sum of the distances between the two objects to be retained and their CCA is the least;
4. Replace the two objects retained by their CCA;
5. Go back to step one.

In cases in which equal distances remain after step three, both solutions are indicated to allow exploration of both of them (this did not happen; see Appendices).

The principal inconvenience of this algorithm is that reversal is not allowed. On the other hand, it is fast, and permits the handling of very large tables with a very small microcomputer. The branches farthest from the root are relatively stable, and well resist changes in characters or in objects; but the lowest nodes, near the root, do not. This is why two runs are necessary for large tables: the first one allows choice of the main branches after the next step described below, and the second takes the CCAs of the groups retained after the first run.

The second algorithm tried uses the distances between pairs of objects and their CCAs: it starts with two objects such that the sum of the distances between them and their CCA is minimal, replaces the two objects by their CCA and starts again. It uses much more computer time than the first algorithm because all the distances must be recalculated every time, and tends to root those objects that are a little farther from the others than the average distance directly to the basal node of the tree. As a result, the tree is generally longer than that built with the former algorithm. However, the final result is not different after the next step, but requires much more time.

To find non-minimum paths, the table including the objects and nodes of the minimum tree is then scanned, to determine all possible filiation relationships among the nodes, such a relation being possible when one of the two objects or nodes under consideration has all its indices at most equal to those of the other object or node, and at least one index lower. This procedure allows one to draw a network of possible phylogenetic relationships, constituted by the tree obtained in the former step as well as the new paths so determined.

In order of preference, the criteria used to justify the choices among several possible origins are these:

1. Occurrence of a synapomorphy *s.s.;*
2. Suppression of a node representing an object not included in the primitive data set,

without increase in the number of multiple nodes;

3. Occurrence of a rare homoplasy;
4. Similarity in characters of which the functional value has not been demonstrated;
5. Overall similarity;
6. Geographical distribution.

In practice the choice is more difficult whenever the sum of the indices of the objects is close to either the theoretical maximum (advanced apomorphy in many characters), or the theoretical minimum, which is the CCA of all the objects and the root of the tree (many plesiomorphic states). This difficulty is foreseeable in theory: the late Pierre Delattre (unpublished) showed that, when one makes a system in which all possible homoplasies are admitted, including all the possible evolutionary paths from plesiomorphic to apomorphic state for all characters, the taxonomic objects represented along the most numerous paths are those that are relatively close to the objects of which the sum of the indices is the theoretical maximum or the theoretical minimum. If synapomorphies cannot be found, the solution might be to seek characters of which the states are plesiomorphic in the objects having many apomorphies, and apomorphic in the objects having many plesiomorphies, to bring the sum of the indices close to the median between the theoretical maximum and minimum, and to provide the best possible discrimination between the possible paths.

The data sets of Appendix F were treated with the program described, and with the PENNY program of the PHYLIP package, version 2.5 (1984) (Felsenstein, 1982). The latter builds all the possible trees and picks out the shortest one(s); it was run under the same assumptions, i.e. reversal not being allowed, on an HB Mini6 computer.

For the Orthurethra, the shortest tree of 60,000 (3.34% of all possible trees) is 32 steps long and has only one node that was not identified in Text-fig. 21, i.e. the Chondrinidae were placed as the sister group of the Pupillidae- Pyramidulidae- Achatinellidae-Valloniidae group. The minimum tree found after the process described above (and before discussing non-minimum paths, dashed lines in Text-fig. 21), is 33 steps long but required one-tenth of the computer time on a much smaller computer (AppleIIE 64K *vs.* Mini6). The tree retained here after discussion (Text-fig. 22) is 35 steps long.

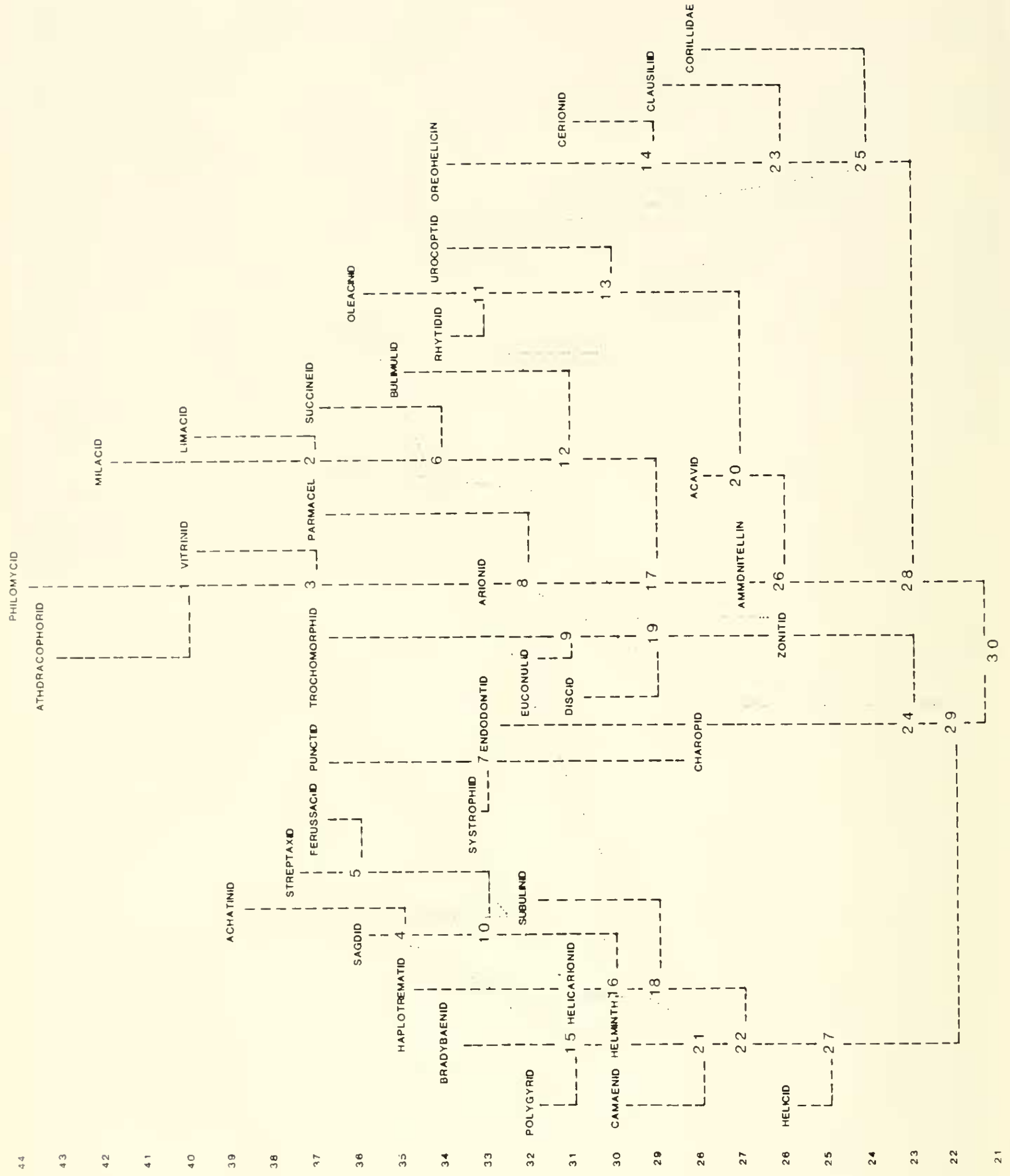
Congruence among the shortest trees found for the non-Orthurethra (five trees 178 steps long, one 163 steps long among 90,000 trees) is worse, but it is no better with any of the classifications of the Pilsbry-Baker school. Among the families of which the position might seem the most dubious in the classification presented below, the Helicarionidae are the sister group of the Camaenidae in the six shortest trees found; the Sagdidae and Haplotrematidae are grouped with the Helminthoglyptidae and Polygyridae in the six trees; the Corillidae are grouped with the Acavidae and Rhytididae in the six trees; the Oreohelicinae are grouped with the Acavidae, Rhytididae and Corillidae in three trees and with some clausilioid families in three trees; the Ammonitellinae are never far from clausilioid families, but form a monophyletic group with some of them in only two trees and never form a monophyletic group with any helicoid family; the Succineidae are included in a monophyletic group lumping some families of aulacopod slugs and semislugs, as in the minimum tree (dashed lines, Text-fig. 23) in the six trees.

Paleobiogeography: As far as possible, the phylogenetic trees presented below have been confronted with paleogeographical data (which in some cases have been used as a test) extracted from the following works: for the Paleozoic: Morel and Irving, 1978; Scotese *et al.*, 1979; for the Mesozoic and Cenozoic: Smith and Briden, 1977; Owen, 1983; for the possibile opening of the Pacific Ocean: Nur and Ben Avraham, 1981.

In every case the paleobiogeographical hypotheses presented below must be used with caution, because: first, some stylommatophoran groups are probably very ancient (Solem & Yochelson, 1979; Solem, 1981), but only very few fossils older than Eocene are available; secondly, even newer fossils are not common, and are virtually unknown outside Europe and North America; thirdly, we know nothing of the anatomy of fossil land snails, and convergence in shell characters is likely; and finally, Paleozoic paleogeographical data are not precise, and to a large extent still under discussion.

Phylogeny and classification of Orthurethra

The occurrence of a synapomorphy, i.e. a kidney both long and divided internally into two distinct regions, allows the independent analysis of the Orthurethra.


PHILOMYCID
ATHORACOPHORID
MILACID
VITRINID
LIMACID
ACHATINID
STREPTAXID
SUCCINEID
PARMACEL
TROCHOMORPHID
PUNCTID
FERUSSACID
OLEACINID
SAGDID
BULIMULID
HAPLOTREMATID
RHYTIDID
UROCOPTID
OREOHELICIN
BRADYBAENID
ARIONID
ENDODONTID
SYSTROPHID
SUBULINID
EUCONULID
POLYGYRID
CERIONID
DISCID
HELICARIONID
HELMINTH
CAMAENID
CLAUSILID
CORILLIDAE
ACAVID
CHAROPID
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TEXT-FIG. 23. Network of possible phyletic relationships among non-orthurethran families. Indices of nodes, Appendix F. Numbers to the left correspond to sums of indices of nodes.

Possible ancestor-descendant relationships between nodes:
Charopidae: Endodontidae, Punctidae, Systrophiidae, =7=.
Arionidae: Philomycinae, Athoracophoridae, Vitrinidae, Milacidae, Limacidae, =1=, =2=, =3=.
Zonitidae: Athoracophoridae, Punctidae, Discidae, Philomycinae, Vitrinidae, Milacidae, Limacidae, Trochomorphidae, Euconulidae, Helicarionidae, Ferussaciidae, Subulinidae, Achatinidae, Oleacinidae, Haplotrematidae, Streptaxidae, Sagdidae, Bradybaenidae, =1=, =2=, =3=, =4=, =5=, =9=, =10=, =16=, =18=, =19=.
Euconulidae: Punctidae.
Helicarionidae: Athoracophoridae, Philomycinae, Vitrinidae, Limacidae, Achatinidae, Haplotrematidae, Sagdidae, =1=, =3=, =4=.
Subulinidae: Achatinidae.
Acavidae: Athoracophoridae, Rhytididae.
Cerionidae: Vitrinidae.
Polygyridae: Sagdidae.
Camaenidae: Achatinidae.
Ammonitellinae: Succineidae, Athoracophoridae, Arionidae, Philomycinae, Vitrinidae, Parmacellidae, Milacidae, Limacidae, Ferussaciidae, Achatinidae, Oleacinidae, Bulimulidae, Streptaxidae, Sagdidae. =1=, =2=, =3=, =5=, =6=, =8=, =11=, =12=, =17=.
Bradybaenidae: Achatinidae.
Helminthoglyptidae: Milacidae, Limacidae, Achatinidae, Polygyridae, Sagdidae, Bradybaenidae, =2=, =4=, =15=.
Helicidae: Succineidae, Athoracophoridae, Arionidae, Philomycinae, Vitrinidae, Parmacellidae, Milacidae, Limacidae, Ferussaciidae, Achatinidae, Oleacinidae, Bulimulidae, Streptaxidae, Sagdidae, =1=, =2=, =3=, =4=, =5=, =6=, =8=, =10=, =12=, =17=.
= 1= : Athoracophoridae, Philomycinae.
= 2= : Milacidae, Limacidae.
= 3= : Athoracophoridae, Philomycinae, Vitrinidae, =1=.
= 4= : Achatinidae, Sagdidae.
= 5= : Ferussaciidae, Streptaxidae.
= 6= : Succineidae, Milacidae, Limacidae, =2=.
= 7= : Punctidae, Systrophiidae.
= 8= : Athoracophoridae, Arionidae, Philomycinae, Vitrinidae, Parmacellidae, Milacidae, Limacidae, =1=, =2=, =3=.
= 9= : Punctidae, Trochomorphidae, Euconulidae.
=10= : Ferussaciidae, Achatinidae, Streptaxidae, Sagdidae, =4=, =5=.
=11= : Oleacinidae, Rhytididae, Streptaxidae.
=12= : Succineidae, Philomycinae, Vitrinidae, Milacidae, Limacidae, Bulimulidae, =2=, =6=.
=13= : Philomycinae, Vitrinidae, Limacidae, Ferussaciidae, Oleacinidae, Urocoptidae, Rhytididae, Streptaxidae, =5=, =11=
=14= : Vitrinidae, Cerionidae, Oreohelicinae.
=15= : Limacidae, Achatinidae, Polygyridae, Sagdidae, Bradybaenidae, =4=.
=16= : Athoracophoridae, Philomycinae, Vitrinidae, Limacidae, Helicarionidae, Ferussaciidae, Achatinidae, Haplotrematidae, Streptaxidae, Sagdidae, =1=, =3=, =4=, =5=, =10=.
=17= : Succineidae, Athoracophoridae, Arionidae, Philomycinae, Vitrinidae, Parmacellidae, Milacidae, Limacidae, Bulimulidae, =1=, =2=, =3=, =6=, =8=, =12=.
=18= : Athoracophoridae, Philomycinae, Vitrinidae, Limacidae, Helicarionidae, Ferussaciidae, Subulinidae, Achatinidae, Oleacinidae, Haplotrematidae, Streptaxidae, Sagdidae, Bradybaenidae, =1=, =3=, =4=, =5=, =10=, =16=.
=19= : Punctidae, Discidae, Vitrinidae, Limacidae, Trochomorphidae, Euconulidae, =9=.
=20= : Athoracophoridae, Philomycinae, Vitrinidae, Limacidae, Ferussaciidae, Oleacinidae, Acavidae, Cerionidae, Urocoptidae, Rhytididae, Streptaxidae, =1=, =3=, =5=, =11=, =13=.
=21= : Athoracophoridae, Philomycinae, Vitrinidae, Milacidae, Limacidae, Helicarionidae, Achatinidae, Haplotrematidae, Polygyridae, Sagdidae, Camaenidae, Bradybaenidae, Helminthoglyptidae, =1=, =2=, =3=, =4=, =15=.
=22= : Athoracophoridae, Philomycinae, Vitrinidae, Milacidae, Limacidae, Helicarionidae, Ferussaciidae, Subulinidae, Achatinidae, Oleacinidae, Haplotrematidae, Streptaxidae, Polygyridae, Sagdidae, Camaenidae, Bradybaenidae, Helminthoglyptidae, =1=, =2=, =3=, =4=, =5=, =10=, =15=, =16=, =18=, =21=.
=23= : Athoracophoridae, Philomycinae, Vitrinidae, Parmacellidae, Limacidae, Ferussaciidae, Clausiliidae, Oleacinidae, Bulimulidae, Cerionidae, Urocoptidae, Rhytididae, Streptaxidae, Oreohelicinae, =1=, =3=, =5=, =11=, =13=, =14=.
=24= : Succineidae, Athoracophoridae, Endodontidae, Charopidae, Punctidae, Discidae, Philomycinae, Vitrinidae, Zonitidae, Milacidae, Limacidae, Trochomorphidae, Euconulidae, Helicarionidae, Ferussaciidae, Subulinidae, Achatinidae, Oleacinidae, Systrophiidae, Haplotrematidae, Rhytididae, Streptaxidae, Polygyridae, Sagdidae, Camaenidae, Bradybaenidae, Helminthoglyptidae, =1=, =2=, =3=, =4=, =5=, =6=, =7=, =9=, =10=, =11=, =15=, =16=, =18=, =19=, =21=, =22=.
=25= : Athoracophoridae, Philomycinae, Vitrinidae, Parmacellidae, Limacidae, Ferussaciidae, Clausiliidae, Oleacinidae, Bulimulidae, Cerionidae, Urocoptidae, Rhytididae, Streptaxidae, Corillidae, Oreohelicinae, =1=, =3=, =5=, =11=, =13=, =14=, =23=.
=26= : Succineidae, Athoracophoridae, Arionidae, Philomycinae, Vitrinidae, Parmacellidae, Milacidae, Limacidae, Ferussaciidae, Oleacinidae, Acavidae, Bulimulidae, Cerionidae, Urocoptidae, Rhytididae, Streptaxidae, Ammonitellinae, Oreohelicinae, =1=, =2=, =3=, =5=, =6=, =8=, =11=, =12=, =13=, =14=, =17=, =20=.
=27= : Succineidae, Athoracophoridae, Arionidae, Philomycinae, Vitrinidae, Parmacellidae, Milacidae, Limacidae, Helicarionidae, Ferussaciidae, Subulinidae, Achatinidae, Oleacinidae, Bulimulidae, Haplotrematidae, Streptaxidae, Polygyridae, Sagdidae, Camaenidae, Bradybaenidae, Helminthoglyptidae, Helicidae, =1=, =2=, =3=, =4=, =5=, =6=, =8=, =10=, =12=, =15=, =16=, =17=, =18=, =21=, =22=.
=28= : Succineidae, Athoracophoridae, Endodontidae, Punctidae, Arionidae, Philomycinae, Vitrinidae, Parmacellidae, Milacidae, Limacidae, Ferussaciidae, Clausiliidae, Oleacinidae, Acavidae, Bulimulidae, Cerionidae, Urocoptidae, Rhytididae, Streptaxidae, Corillidae, Ammonitellinae, Oreohelicinae, =1=, =2=, =3=, =5=, =6=, =8=, =11=, =12=, =13=, =14=, =17=, =20=, =23=, =25=, =26=.
=29= : Succineidae, Athoracophoridae, Endodontidae, Charopidae, Punctidae, Discidae, Arionidae, Philomycinae, Vitrinidae, Zonitidae, Parmacellidae, Milacidae, Limacidae, Trochomorphidae, Euconulidae, Helicarionidae, Ferussaciidae, Subulinidae, Achatinidae, Oleacinidae, Bulimulidae, Systrophiidae, Haplotrematidae, Rhytididae, Streptaxidae, Polygyridae, Sagdidae, Camaenidae, Ammonitellinae, Oreohelicinae, Bradybaenidae, Helminthoglyptidae, Helicidae, =1=, =2=, =3=, =4=, =5=, =6=, =7=, =8=, =9=, =10=, =11=, =12=, =15=, =16=, =17=, =18=, =19=, =21=, =22=, =24=, =27=.

Phylogeny: As already emphasized, my sampling of the Orthurethra is probably not sufficient and I am consequently reluctant to trust my results. Taking more species belonging to more genera into account would possibly allow classes (and therefore character states) of lesser amplitude and increase the reliability of the results.

The 11 family-level taxa analyzed share one synapomorphy and several symplesiomorphies that have been eliminated from the data set: synapomorphic length of the kidney (LR2′), symplesiomorphic spheroid buccal mass (BM1), absence of an oesophageal crop (OC1), relatively short intestine (IL1), absence of ureteric tube (UR1), position of the right parietal ganglion (PAD1). The characters remaining are: gastric crop shape (SC), degree of differentiation of the gastric pouch (PS), and the remaining characters of the nerve ring (CC, CPD, CPR, PLD, PLG, VG, PAG, FG).

Possible phyletic relationships are shown in Text-fig. 21, the data set and the coordinates of the calculated nodes are given in Appendix F, and the list of all the possible filiations between the nodes is given in the caption of Text-fig. 21.

A first remark, which might seem surprising because the Achatinellidae and Partulidae have often been considered the most "primitive" of the Stylommatophora (Boss, 1982), is that the Valloniidae are the most plesiomorphic for the largest number of characters and might have been isolated very early. They also exhibit a plesiomorphy unique among the Stylommatophora, i.e. the position of the genital opening relatively far back. As discussed by Watson (1915), the same arrangement is probably related to carnivory and therefore apomorphic in some rhytidids, which does not seem to be the case in the valloniids. These numerous plesiomorphies of the valloniidae might result from their trend to paedomorphosis; however this is probably not the case, because of the position of the genital pore, which is plesiomorphic (Tillier, 1984b) but not paedomorphic, the genital apparatus developing very late in ontogeny without any described displacement of the genital opening.

The early differentiation of the Chondrinidae is also likely if, as suggested above, the family includes two groups of which one is Holarctic and the other exclusively Gondwanian.

Two paths can be chosen without too much hesitation among the possibilities shown in Text-fig. 21. The first is the common origin of the Cochlicopidae and Amastridae. This option allows the suppression of node 2, and groups together not only the Cochlicopidae and Amastridae (classical group), but also the Partulidae and Enidae. The latter group corresponds to the classification by Solem (1978), and can be accepted because the trend to visceral mass shortening occurs in these two families alone among the Orthurethra; furthermore, it is biogeographically coherent inasmuch as the Central and South Pacific Partulidae might be derived from some Oriental or western Pacific Cerastuinae. The second is the common origin of the Pupillidae and Pyramidulidae. It seems clear to me that these two groups differ only in their shell shape.

Monophyly of the Valloniidae and Vertiginidae can be rejected inasmuch as, within the Orthurethra the position of the right pleural ganglion close to the right cerebral ganglion (PLD2) appears to be a synapomorphy of the group that includes the Valloniidae but not the Vertiginidae.

My knowledge of the Orthurethra is insufficient to allow me to discuss the other possible relationships. In particular I have no support other than previous classifications to reject the monophyly of the Orculidae, Amastridae and Cochlicopidae. The tree constructed on the basis of these accepted hypotheses is shown in Text-figure 22.

Classification: The tree retained divides the Orthurethra into two groups, which are defined and subdivided on the basis of characters of the nervous system: digestive tract morphology appears only once as a synapomorphy, not unique, uniting the Pupillidae and the Pyramidulidae. I do not trust this tree enough to give names to these two groups, and I shall call Group I the group including the Pupillidae, Pyramidulidae, Achatinellidae and Valloniidae; and Group II the group including the Orculidae, Vertiginidae, Amastridae, Cochlicopidae, Partulidae, Enidae and Chondrinidae (Text-fig. 22).

Group I is based on the synapomorphic proximity of the right pleural ganglion to the right cerebral ganglion and on the primary shortening of the cerebral commissure. Group II is based on the synapomorphic shortening of the cerebro-pedal connectives. Apart from these character states, the distinction between the two groups represents two different patterns in nerve ring shortening. Group I is characterized by shortening of the nerve ring primarily through shortening of the cerebral commissure and of the cerebropleural connectives, the cerebro-pedal connectives keeping their plesiomorphic length and asymmetry (except in the Valloniidae): shortening is primarily in the dorsal portion of the nerve ring. Group II is characterized by primary shortening of the lateral connectives, whereas the upper portion of the nerve ring primarily keeps its plesiomorphic arrangement. Most individual apomorphic states are found in both groups: it is their succession and the resulting evolutionary sequence in the arrangement of the nervous system that define the groups, which would ultimately converge in a single arrangement if evolution were pursued further in compaction of the nervous system.

Speculations on history of Orthurethra: If the taxonomic distinction established by Solem and Yochelson (1979) between the Carboniferous Dendropupinae and Anthracopupinae, attributed by them respectively to the Enidae and Achatinellidae, is reliable, then by implication groups I and II were already differentiated. Their differentiation through isolation in Gondwana and Laurasia, before the formation of Pangea, is then possible. If it occurred, group II is the best candidate for differentiation in Gondwana, because it contains the only orthurethran group that is exclusively Gondwanian (Hypselostomatinae, *Fauxulus, Gibbulina, Ulpia*). This hypothesis coincides with the early differentiation of the Chondrinidae, shown in Text-fig. 22. The Chondrinidae appeared in Europe during the Eocene, that is, later than most of the other orthurethran families, which are at least as old as Paleocene; this might be due to late migration northward through the Panamanian region, whereas the other families belonging to group II would have been differentiated in the Laurasian region after the opening of the Tethys Sea.

The other families of group II, Amastridae and Partulidae excepted, did occur in Europe during the Paleocene. One can therefore suppose that they occurred also in North America, where they all became extinct (unless one admits that the only Recent species now occurring in North America, *Cochlicopa lubrica,* already occurred). Some Enidae, close in shell morphology to Recent Cerastuinae, did appear first in Laurasia, possibly during the Carboniferous (unless the Dendropupinae represent the stem-group of the non-chondrinid members of group II). During the Miocene this stock could colonize East Africa through Arabia, and the Indo-Malayan Archipelago down to Queensland, New Caledonia and possibly Vanuatu (ancestors of the Recent Cerastuinae). Some members of this group and some Cochlicopidae colonized the Central Pacific islands at a date difficult to determine, where their descendants form respectively the Partulidae and Amastridae. At some time between the Eocene and the Miocene, the primitive stock of the Enidae had been replaced in Eurasia by the Chondrulinae and Eninae.

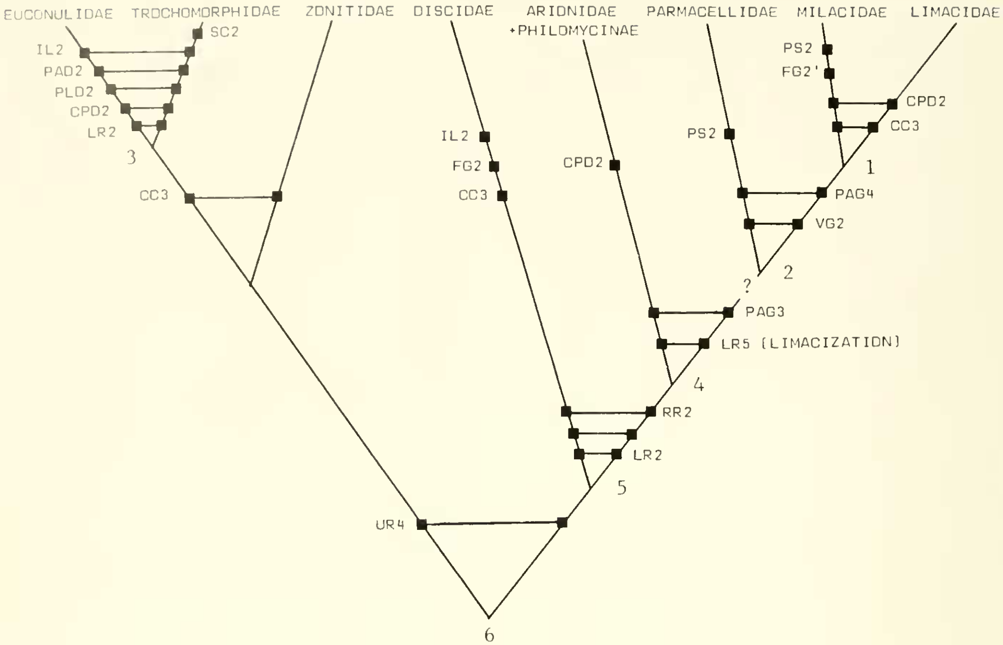
No element indicates the occurrence of any family belonging to group I outside the Laurasian region and the Pacific earlier than recently (dispersal of the Pupillidae is very easy owing to their very small size, and might be quite recent). No element allows the dating of the differentiation of the Valloniidae (between the Carboniferous and the Paleocene), unless one can find a synapomorphy of *Anthracopupa* with the Achatinellidae; in which case the Valloniidae would be as old as Carboniferous. The Recent forms of the Pupillidae-Pyramidulidae group seem to have appeared during the Eocene, but the actual date of the separation between the ancestors of this group and those of the Achatinellidae, and the date of colonization of the Pacific Islands by the latter remains a mystery.

Phylogeny and classification of non-orthurethran Stylommatophora

Possible relationships of families and superfamilies are represented in Text-fig. 23. Only the paths to be discussed are shown, to avoid confusion in the diagram (non-minimum paths that result in multiple nodes generally are without interest). The complete list of possible paths between the nodes of the primary tree is given in the caption of Text-fig. 23.

Zonitoidea: The Zonitoidea include the families Zonitidae, Trochomorphidae, Parmacellidae, Limacidae, Milacidae, Euconulidae, Discidae and Arionidae (including the Philomycinae).

Although the group did not occur in any of the shortest trees produced either here (Text-fig. 23, dashed lines) or by the PENNY algorithm, it is probably not worth discussing the grouping of the first five of these families, which has long been admitted, and against which I cannot at present think of any argument (Zonitidae, Trochomorphidae, Parma-



TEXT-FIG. 24. Minimum tree of possible phyletic relationships among zonitoid families (retained; ? = position doubtful).

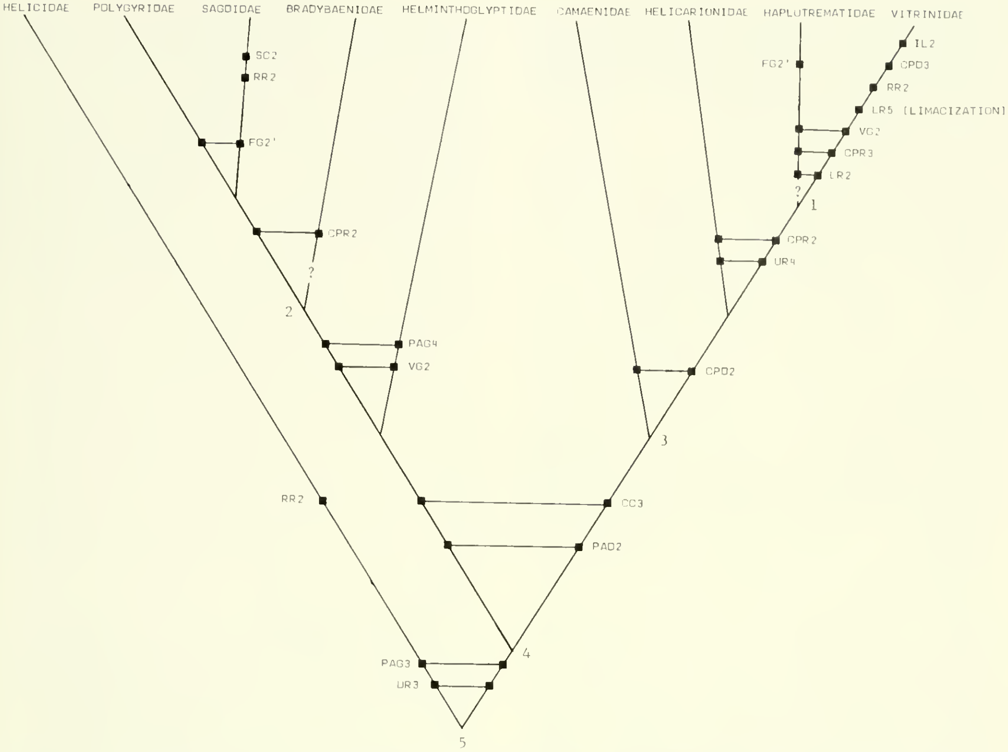
cellidae, Limacidae, Milacidae). I have no arguments other than nomenclatural stabiilty and geographical distribution in favor of this group.

Inclusion of the families Euconulidae and Discidae in the Zonitoidea is justified not only by the scheme shown in Text-fig. 23, but also by overall similarity (Text-fig. 20). Close relationships between the Euconulidae and Zonitidae have already been suggested (Van Mol & Van Bruggen, 1971), based on similarity in some genital characters (glandular area occurring along the vagina, and not along the free oviduct as in the Helicarionidae).

Because the Philomycinae differ from the Arionidae only in having more apomorphic character states, and because both groups share a synapomorphy in kidney morphology, grouping them into a single family seems justified. Although members of this group can be easily identified, analyzing their relationships with other groups is far less easy. The Arionidae are grouped here with the Discidae within the Zonitoidea because the Arionidae and Discidae differ very little in characters unrelated to limacization.

Character states of the CCA of the Zonitoidea are plesiomorphic for all characters except the closure of the ureteric tube, which is always complete (UR4).

The tree built from the diagram of the possible relationships of the zonitoid families has two groups (Text-fig. 24). One includes the Zonitidae, Euconulidae and Trochomorphidae; the other includes the Discidae, the Arionidae and the three other slug families. The latter group is characterized by kidney shortening and internal dedifferentiation (LR2, RR2), displacement of the right parietal ganglion toward the visceral ganglion (PAD2), and perhaps loss of the amatorial organ. The synapomorphies uniting the four slug families are only character states that are probably related to limacization (LR5, PAG3); it is also possible that the Discidae and Arionidae form a monophyletic group. The families Parmacellidae, Limacidae and Milacidae share the median position of the visceral ganglion (VG2), and compaction in the left portion of the visceral chain (PAG4). These three families are placed there on the tree probably only because limacization results in a shorter distance from the arionid slugs than from any other zonitoid family; it is also possible that there are two groups on this side of the tree, i.e. the Arionacea (Arionidae + Discidae) and



TEXT-FIG. 25. Minimum tree of possible phyletic relationships among helicoid families (doubtful: see text).

the Limacacea (Limacidae + Milacidae + Parmacellidae + ?Trigonochlamydidae); or, possibly more consistently, the Discidae + Arionidae constitute the sister group of all other zonitoid families.

The other group, which might be called the Zonitacea, includes the family Zonitidae, which exhibits plesiomorphy in nearly all its observed character states, and of which the monophyly may hardly be justified. However, cerebral commissure shortening and occurrence of a glandular zone along the vagina might constitute synapomorphies of the group composed of the Zonitidae, Trochomorphidae and Euconulidae within the Zonitoidea. The Euconulidae and Trochomorphidae share apomorphies in kidney length (LR2), nerve ring (CPD2, PLD2, PAD2), and intestinal length (IL2). Absence of a vaginal glandular zone might be a synapomorphy of the Trochomorphidae within this group, whereas the Euconulidae are characterized by the position of the spermathecal insertion (Baker, 1941).

The only clear points in the history of the Zonitoidea are that the group is probably Laurasian in origin, and that the families were probably already differentiated in the Paleocene in Europe and North America. The Euconulidae (*Afroconulus*) and the Arionidae (*Oopelta*) might have colonized eastern Africa from Arabia during the Miocene, when the Tethys Sea was closed in this region (like the Cerastuinae, Helicidae and possibly the Achatinoidea). The tree presented in Text-fig. 24 implies that the Carboniferous genus *Protodiscus* is probably not a member of the Recent family Discidae, but at most a disciform primitive zonitoid: the characters upon which Solem and Yochelson (1979) base their familial attribution of *Protodiscus* to the Discidae might be at best synapomorphies of the zonitoids, and at worst symplesiomorphies of the latter (= synapomorphies of the non-orthurethran Stylommatophora?).

As explained below, I have placed the Helicarionidae and Vitrinidae in the Helicoidea for the sake of further discussion. However, their inclusion in the Zonitoidea would modify very little the tree of Text-fig. 24: the Helicarionidae would originate from a triple node at which the Zonitidae and Euconulidae + Trochomorphidae originate; the Vitrinidae, if not derived from the Helicarionidae (Text-fig. 23), would originate between the Parmacellidae and Milacidae (Text-fig. 24).

Helicoidea: The Helicoidea include the families Helicidae, Helminthoglyptidae, Bradybaenidae, Camaenidae, Polygyridae, Haplotrematidae, Sagdidae, Helicarionidae and Vitrinidae. Grouping together the first four of these families is classical (Zilch, 1959–1960), although rejected by Solem (1978) and Boss (1982), who prefer to group the Polygyridae with the Corillidae, and the Oreohelicidae with the Ammonitellidae into a distinct superfamily. These last three families being considered here acavoid (*v. infra*), and nobody doubting the relative proximity of the Polygyridae, Camaenidae and remaining Helicoidea, the shortest tree in Text-fig. 23 is accepted here.

Placing the Sagdidae among the Helicoidea has been discussed above and seems better to me than placing them among the Achatinoidea, which, however, is more acceptable in terms of phyletic distance (Text-fig. 23): *Sagda* has an apomorphy common among the Helicoidea, apparent fusion of the visceral and left parietal ganglia, and does not have a synapomorphy of the Achatinoidea, the absence of an amatorial organ. In this interpretation the penial appendix of *Sagda* is homologous with the amatorial organ of the helminthoglyptids from which it seems to differ only in position, not in morphology.

Placement of the Helicarionidae among the Helicoidea is more a challenge than a certitude. Their position in either the Helicoidea or Zonitoidea does not modify the relative position of the superfamilies discussed below, and their placement among the Helicoidea provides shorter trees than placement among the Zonitoidea, whatever the computer program used. The position of the Vitrinidae, which are much closer to the Helicarionidae than to the Zonitidae in terms of both phyletic distance (Text-fig. 23) and phenetic distance (Text-fig. 20), is the consequence of this choice; diversity of the Vitrinidae is relatively high in East Africa, where one part of the Helicarionidae perhaps originated (*v. infra*). However, the Vitrinidae have surprisingly many apomorphic character states even though their degree of limacization is slight, facts that make the discussion of their affinities more uncertain.

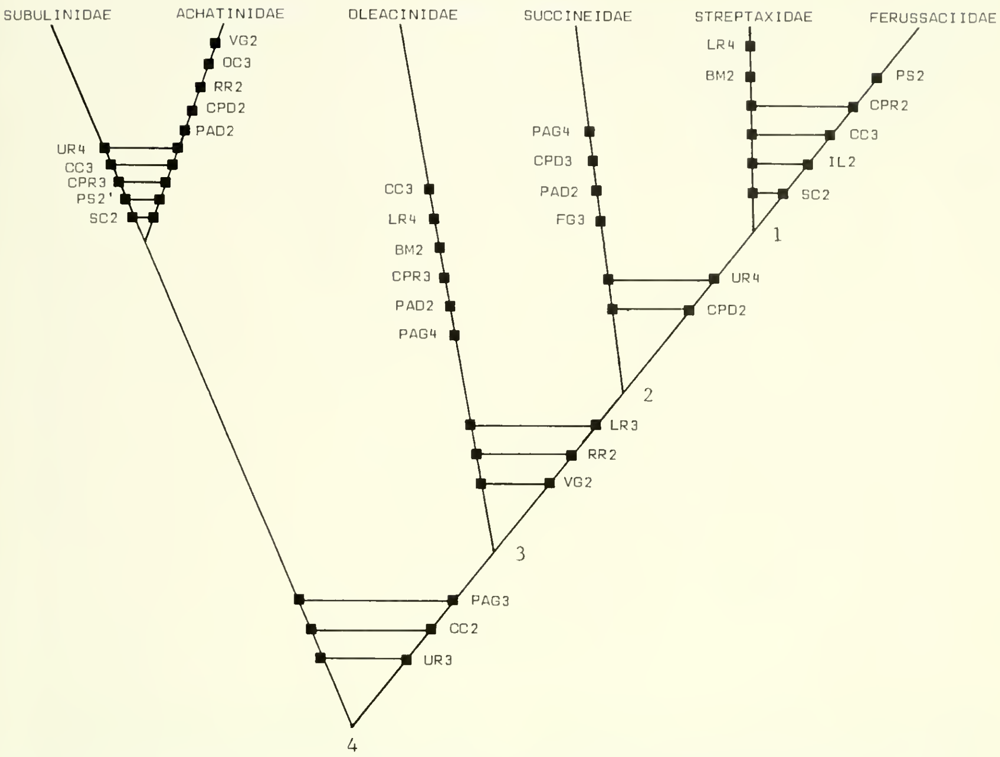
Placing the Haplotrematidae among the Helicoidea is also questionable, for they resemble much less any helicoid family than they do the Oreohelicidae, which are here considered members of the Acavoidea (Text-fig. 20); they might be the North American representatives of the carnivorous trend in the acavoids. They are placed here among the Helicoidea not only because this solution provides shorter trees, but also because *Haplotrema* has the apparent fusion of the visceral and left parietal ganglia seen in many helicoids but in no oreohelicid.

The Oreohelicidae are here removed from the Helicoidea, because: first, in all the shortest trees obtained, they are grouped with the Acavoidea; and second, this position makes sense in view of the way in which the very short kidney associated with the very short ureteric tube commonly found in the family (Figs. 493, 494, 500, 501) can be integrated into a macroevolutionary pattern at suprafamilial levels (*v. infra*).

The synapomorphies of the Helicoidea so defined are the occurrence of a ureteric tube closed at least to the recto-renal angle of the lung roof (UR3), and the contact between the left parietal and visceral ganglia (PAG3).

The tree shown in Text-fig. 25 must be viewed with caution, because the monophyly of the Helicidae and Helicarionidae is far from certain, and the inclusion of some families is perhaps dubious. However, removing the Helicarionidae and Vitrinidae from the data set modifies only the relative position of the Haplotrematidae, which become the sister group of the Polygridae + Sagdidae. Introducing the Oreohelicidae results only in their placement in the tree as the sister group of all the other families.

The Helicoidea are primarily Laurasian: the South American helminthoglyptids (Parodiz, 1969), African helicids, and Australasian camaenids are probably Late Tertiary immigrants. If the Vitrinidae and Helicarionidae form a monophyletic group, this group might have originated before the Late Cretaceous (European *Provitrina*), and dispersed into Africa and Australasia before the extinction of the Helicarionidae in Europe; the absence of the Helicarionidae from America is problematic, however, and it might be that the Urocyclinae and Gymnarioninae in East Africa and the other subfamilies in the Orient were derived independently from various helicoids. If monophyletic, the Helicarioninae might have been differentiated in Eurasia before the other



TEXT-FIG. 26. Phyletic trees of achatinoid families. 26A) minimum tree. 26B) tree retained (see text).

subfamilies and during the Miocene colonized East Africa and Madagascar on the one hand, and Australasia on the other hand before becoming extinct farther north; their monophyly cannot be argued seriously before the family is revised.

Achatinoidea: The Achatinoidea include the families Achatinidae, Subulinidae, Ferussaciidae, Oleacinidae, Succineidae and Streptaxidae (Text-fig. 23). Although they resemble more some aulacopod families (Text-fig. 20), the Succineidae are tentatively included here on the basis of their special similarities with the Ferussaciidae, i.e. heterurethry (apomorphic) and occurrence of two procerebral commissures (symplesiomorphy unique among the Stylommatophora, as far as known). The Streptaxidae differ from the Ferussaciidae only in their very long lung (shortened in the Ferussaciidae), their internal kidney morphology, and character states related to carnivory.

Synapomorphic character states in the Achatinoidea are the closure of the ureteric tube (UR4), short cerebral commissure (CC2), the contiguity of the left parietal ganglion with the visceral ganglion (PAG3), and possibly the symmetry of the cerebro-pedal connectives (CPR2; only exception occurs in the Succineidae). To distinguish the Achatinoidea from the Helicoidea, the absence of an amatorial organ (and the shell shape?) must be added.

By considering characters not included in the data set used to build the tree shown in Text-fig. 26A, the tree shown in Text-fig. 26B is obtained. Here the Oleacinidae are the sister group of the Ferussaciidae because they share derived states in internal and external morphology of the kidney, and the Succineidae are the sister group of this group because all three families share their trend to heterurethry. The Streptaxidae are the next sister group, without lung shortening, and the Achatinidae and Subulinidae are the sister group of all the others, having no kidney shortening at all.

Given that the achatinoid families, the family Achatinidae excepted, were differentiated

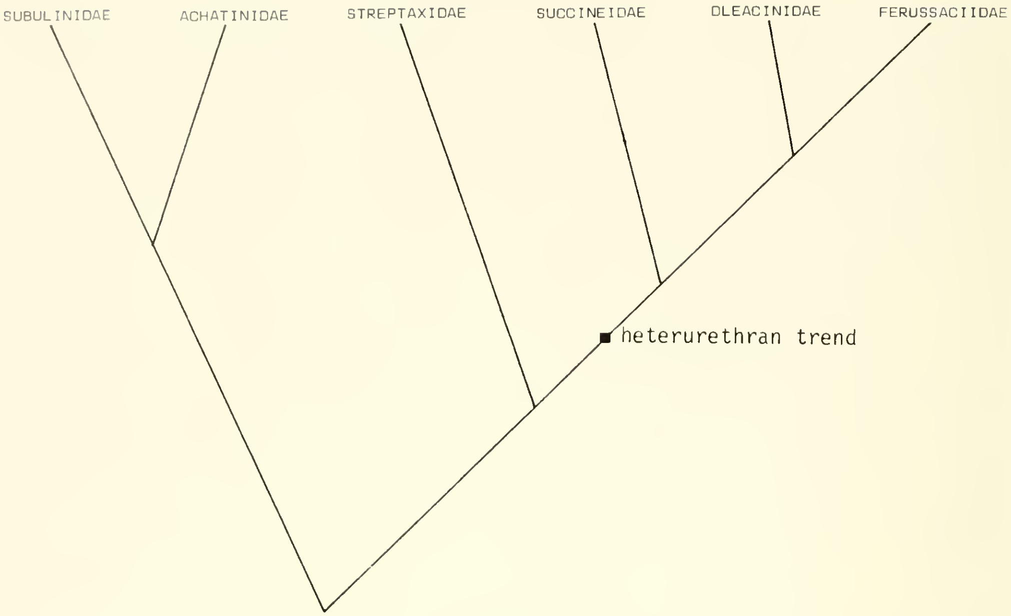
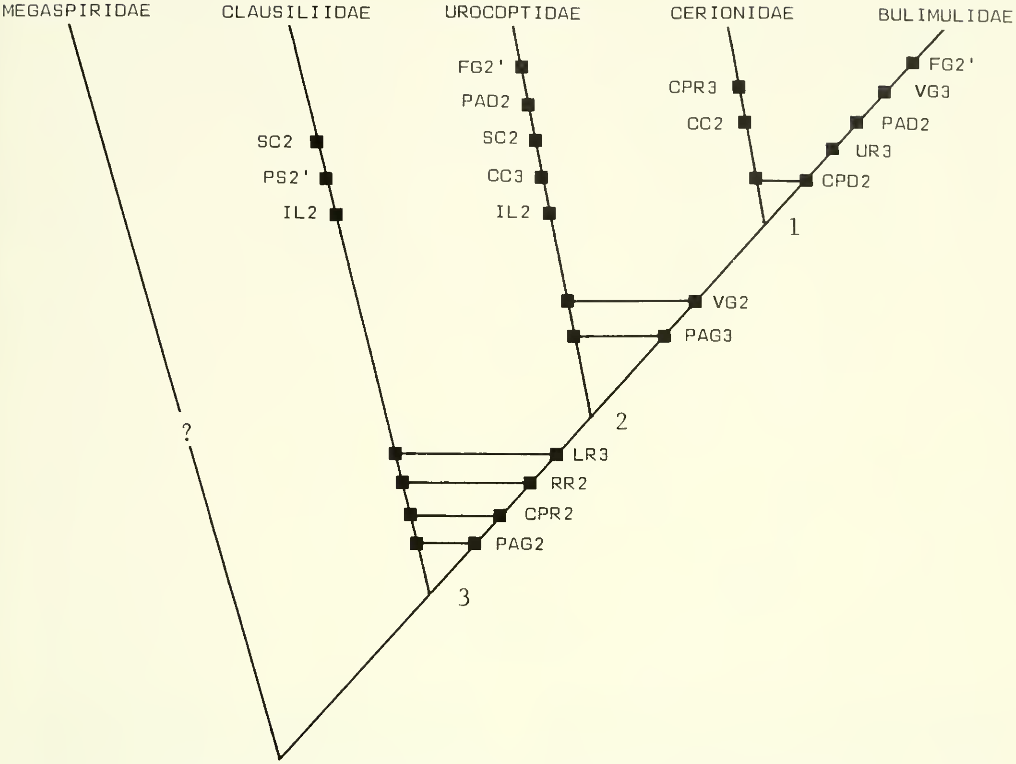


Fig. 26b

in the Eocene in Europe, two scenarios are possible. If the superfamily is Laurasian in origin, these families might have invaded South America through North America. The same, Oleacinidae excepted, might have invaded the Orient and, during the Miocene, Africa, where the Achatinidae might have been derived from the Subulinidae. The alternative solution is to consider the Achatinoidea as Gondwanian in origin: some Streptaxidae, Subulinidae and the common ancestor of the Oleacinidae, Ferussaciidae and Succineidae would have invaded Europe before the Eocene via the Panamanian region and North America; the Subulinidae and Streptaxidae would be vicariant in South America, Africa and the Orient, and the Achatinidae would have appeared in Africa later than the opening of the South Atlantic and than the drift of the Indian plate away from Africa, i.e. later than the end of the Cretaceous. This solution does not explain the quasi-total absence of the Achatinoidea from the Australasian region; the hypothesis of a Laurasian origin, which is also supported by the tree presented below (Text-fig. 29), seems preferable.

Clausilioidea: The Clausilioidea include the families Clausiliidae, Cerionidae, Urocoptidae and Bulimulidae. In the absence of any new element, I follow Pilsbry (1904) and include also the Megaspiridae. Choosing the non-minimum paths that allow this grouping (Text-fig. 23) leads to a multiple node (node 23). However, this group might be formed because at least some members of the various families composing the superfamily form an almost perfect morphocline in many characters: the Cerionidae look exactly like Clausiliidae with a shortened nerve ring (and without a clausilium); within the Urocoptidae *Urocoptis* and *Macroceramus* have the general morphology seen in *Cerion*, whereas *Berendtia* is similar to bulimulids in general anatomy. Furthermore, the Urocoptidae and Bulimulidae have a possible synapomorphy, the apparent fusion of the visceral and left parietal ganglia. The synapomorphic character states of the superfamily are: LR3 RR2 CPR2 PAG2.

In the minimized diagram of possible relationships within the superfamily (Text-fig. 27A), the Cerionidae are the sister group of the Bulimulidae on the basis of the shortening of the cerebro-pedal connectives in both families. I prefer to consider the Urocoptidae the sister group of the Bulimulidae, because both have a tendency to fusion of the visceral and left parietal ganglia, and because of the striking similarity among some members of both families. Two scenarios can be inferred from the tree so constructed (Text-fig. 27B), given that the Clausiliidae occurred in Europe dur-



TEXT-FIG. 27. Phyletic trees of clausilioid families. 27A) minimum tree. 27B) tree retained (? = position doubtful; see text).

ing the Late Cretaceous, the Urocoptidae occurred in North America during the Paleocene, and the Bulimulidae occurred in South America during the Paleocene (Parodiz, 1969). The first scenario involves a Laurasian origin. The Urocoptidae and Cerionidae would have been differentiated respectively in North America and in the Panamanian region during the Paleocene, and the present distribution of these families and of the South American and Australasian Bulimulidae represents a Paleocene South American and trans-Antarctic track from North America to Tasmania, part of Australia, New Zealand, New Caledonia, the Solomon Islands and Vanuatu. It seems that the clausiliid Neniinae arrived in the Andes in the Late Tertiary (Parodiz, 1969); consequently they would have become extinct in North America more recently. The Megaspiridae might have appeared in Laurasia and have migrated along the same track as the Bulimulidae (Pilsbry, 1904); but if the European Danian *Paleostoa* is closer to the clausiliids than to the megaspirids, the latter might be the Gondwanian sister group of all the other clausilioids. This would imply that the superfamily was differentiated before the break-up of Pangea. The other scenario involves a Gondwanian origin. The Megaspiridae and the ancestral stock of all the other families would have been differentiated within Gondwana, and the Clausiliidae, Cerionidae and Urocoptidae would represent successive immigration waves that issued from this ancestral stock through the Panamanian region. This model does not explain the absence of the Bulimulidae and Megaspiridae from the Ethiopian and Indian regions.

Endodontoidea: The group including the families Charopidae, Endodontidae, Punctidae, and Systrophiidae is formed equally well using phenetic (Text-fig. 20) and phyletic (Text-fig. 23 and PENNY algorithm) distances. The inclusion of the Systrophiidae in the Endodontoidea, which might seem sur-

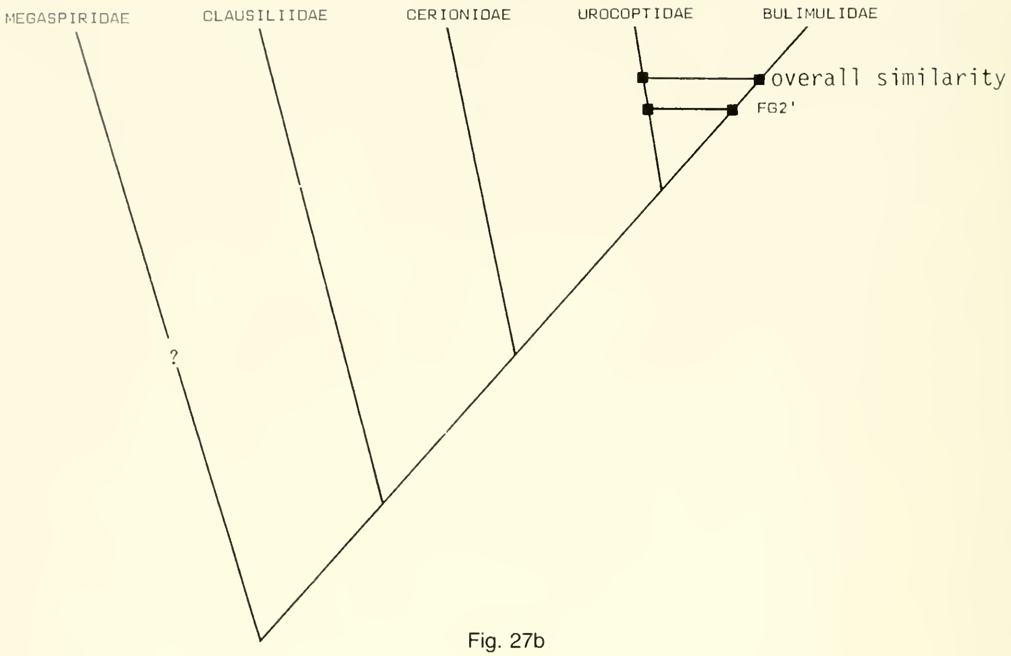
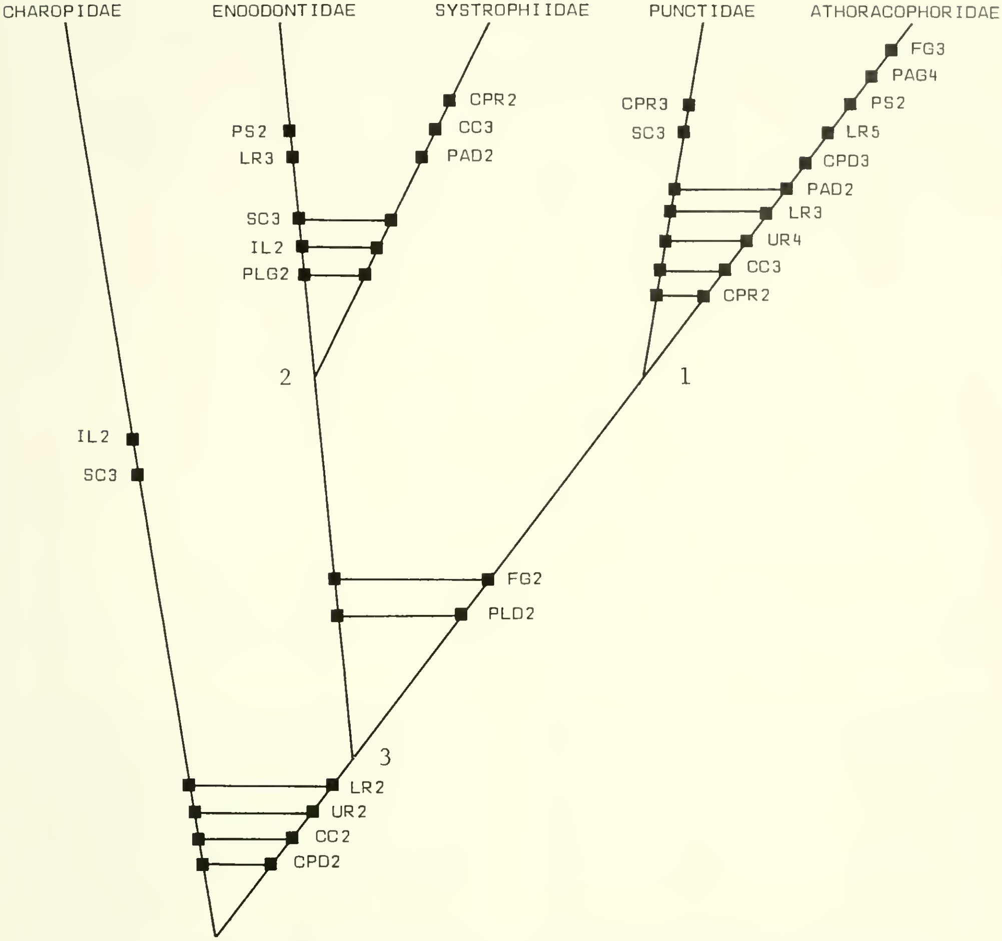


Fig. 27b

prising, has already been proposed by Schileyko (1978a) on a mainly conchological basis. The unique morphology of the nerve ring of the systrophiids might result from the exaggeration of the trends observed in the endodontids (in particular, displacement of the pleural ganglia toward the cerebral ganglia). Weak as the reasons to include the Athoracophoridae in the Endodontoidea might appear, they seem stronger than reasons for placing the family elsewhere. First, of all the taxa studied, the semislug *Cystopelta,* which is here considered to belong to the Punctidae, is closest in anatomy to the Athoracophoridae (Text-fig. 19); this similarity is particularly remarkable because these two taxa represent very different degrees of limacization. Second, this hypothesis is biogeographically coherent: diversity of the Endodontoidea is maximal in the Australasian region.

The synapomorphies of the Endodontoidea so defined are shortening in intestinal length, kidney length, cerebral commissure length and cerebro-pedal connective length (IL2, LR2, CC2, CPD2), and occurrence of a ureteric tube reaching at least the recto-renal angle of the lung (UR2). In the tree constructed from the data set including the CCAs of the endodontoid families (Text-fig. 28), the Charopidae are the sister group of the other families (and possibly the stem group, if one accepts that the shape of the gastric crop of the Athoracophoridae is secondarily plesiomorphic, which is not unlikely). According to this tree, the Charopidae were differentiated from the common ancestor of the other families, which was probably northeast Gondwanian, before the break-up of Gondwana, which resulted in their present distribution. The Charopidae might have spread into the In-donesian Archipelago, via New Guinea, during the Miocene; and North America, via the Panamanian region, during the Cretaceous (unless the superfamily was differentiated before the break-up of Pangea, in which case the North American Charopidae might be a relict of a former Pangean distribution). The Punctidae might have the same history, whereas the Athoracophoridae stayed in the Australasian region. The present distribution of the Punctidae, Athoracophoridae, Endodontidae and Systrophiidae produces a trans-Pacific track when compared with the tree of Text-fig. 28. This track might of course result from dispersal from the west eastward across the Pacific Ocean; but vicariance resulting from the possible opening of this ocean (during the Triassic? Melville, 1981) is also possible. If accepted, this hypothesis leads to the possibility of attributing the present distribution of North and South American charopids to the same event, rather than to



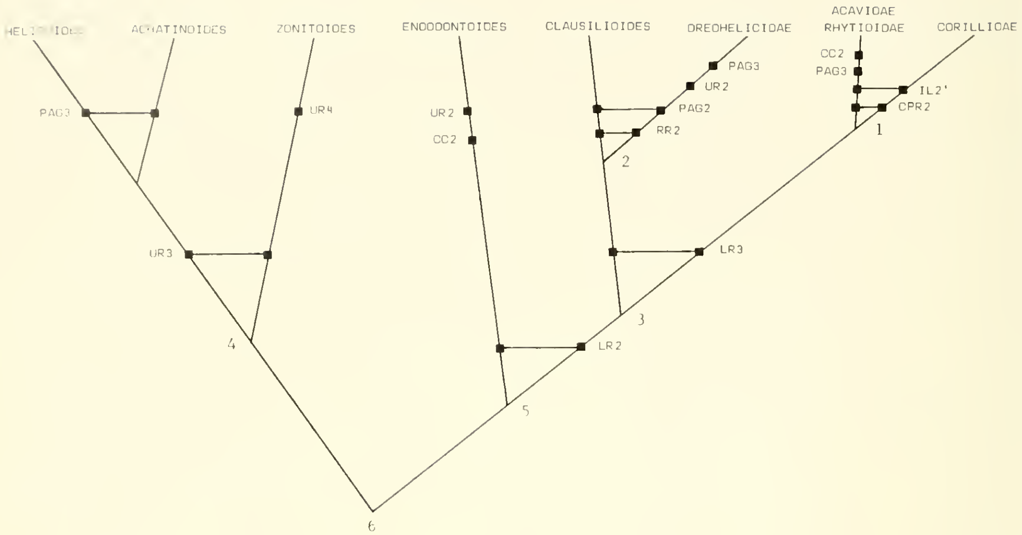
TEXT-FIG. 28. Minimum tree of phyletic relationships among endodontoid families (retained).

Gondwanian vicariance with trans-Panamanian dispersal.

Acavoidea: The superfamily Acavoidea should include at least the families Acavidae and Rhytididae (suppression of nodes 11 and 13, Text-fig. 23). The position of the Oreohelicidae (including the Ammonitellinae) and Corillidae cannot be justified from Text-fig. 23, because they are taken up by the algorithm only at the end of the process of construction of the diagram, and their position is established in relation to nodes that might be modified greatly by the adoption of paths not included in the first short tree. Consequently, their position is discussed and established further from a data set that includes the CCAs of the superfamilies already retained, and the CCAs of the acavoid families. First, however, it should be noted that the four families here considered acavoid have the association of an apomorphic short kidney with a plesiomorphic little- or not-developed ureteric tube, as do the Clausilioidea and Endodontoidea, but not any other superfamily. Including the Oreohelicidae in the Helicoidea does not modify the pattern of relationships between the superfamilies established below.

The synapomorphic character states are: IL2′, LR3 CC2 CPR2 PAG3 for the Acavidae and Rhytididae; IL2′ LR3 RR2 CPR2 PLD2 PAG2 for the Corillidae; and LR3 UR2 RR2 PAG3 for the Oreohelicidae.

The phylogenetic relationships of these families established below (Text-fig. 29) cannot be considered very reliable, principally because of the impossibility of resolving in detail the relationships within the Acavidae-Rhy-



TEXT-FIG. 29. Phyletic trees of non-orthurethran stylommatophoran superfamilies. 29A) minimum tree obtained by introducing acavoid families separately in data set. 29B) tree retained (see text).

tididae. However, all acavoid families but the Oreohelicidae are exclusively Gondwanian, and, vicariance occurring within families, perhaps they originated before the break-up of Gondwana. The Corillidae, which are absent from South America, might have originated after the opening of the South Atlantic Ocean but before the drift of the Indian plate, on which they still occur, i.e. between the earliest Cretaceous and the Cenomanian. If the Oreohelicidae really belong to the Acavoidea, their occurrence in North America might result from either dispersal from South America before or during the Cretaceous; or from trans-Pacific vicariance if the Pacific Ocean opened during the Mesozoic; or from their origin by vicariance in Laurasia, which would imply that the Acavoidea originated before the break-up of Pangea.

Relationships of superfamilies: I discuss next the phyletic relationships of the superfamilies, and describe two new suborders, the Brachynephra and Dolichonephra.

The tree presented in Text-fig. 29A was constructed with the CCAs of the various groups retained above, after the symplesiomorphies and the autapomorphies, which modify the distances without adducing any information about relationships, were eliminated from the data set. This tree divides the Stylommatophora into two groups based on relative chronology in kidney shortening and ureteric tube formation. In the first group, which includes the Endodontoidea, Clausilioidea and Acavoidea, kidney shortening occurs before formation of a ureteric tube. In the second group, which includes the Zonitoidea, Helicoidea and Achatinoidea, the formation of a ureteric tube precedes kidney shortening, if any. This subdivision fits two patterns previously and independently recognized as probable on the basis of functional hypotheses. Furthermore, those superfamilies whose origin was probably Gondwanian are all in the first group, whereas nearly all those whose origin was probably Laurasian are in the second group. The conjunction of this division with hypotheses already entertained independently seems to allow the proposal of their recognition as likely monophyletic suborders: I propose the name *Brachynephra* for the first suborder, including the superfamilies Endodontoidea, Clausilioidea and Acavoidea; and the name *Dolichonephra* for the suborder including the superfamilies Zonitoidea, Helicoidea and Achatinoidea. These names take only the plesiomorphic state in each suborder into account, and do not express fully the fundamental criterion of division, which is the relative chronology of kidney shortening and ureteric tube formation: the kidney is second-

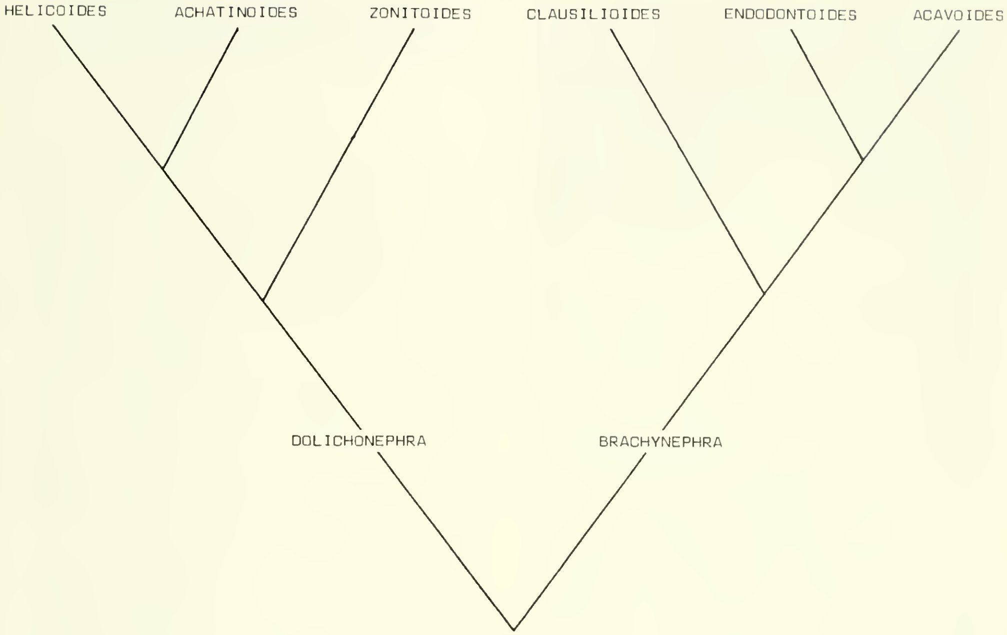


Fig.29b

arily long in the Acavidae and secondarily short in some Achatinoidea if the hypotheses here adopted are true.

The superfamilies included in the Brachynephra are all partly or wholly Gondwanian, as seen above. The apparent monophyly of the Clausilioidea and Oreohelicidae shown in Text-fig. 29A is problematic. One can imagine two explanations of this apparent monophyly. The first is that the tree presented in Text-fig. 29A reflects correctly the history of the suborder: the common ancestor of the Clausilioidea and Oreohelicidae migrated into North America, and was the sister group of the Megaspiridae, which remained Gondwanian but became extinct in Africa and the Indian region. After divergence of the Clausilioidea and Oreohelicidae, the remaining clausilioid families first used their present track southward. If the tree shown Text-fig. 27 is false, the Bulimulidae first occurred in Gondwana after the appearance of the Megaspiridae and before the migration of the ancestor of the other clausilioids and oreohelicids. The second explanation is that the tree in Text-fig. 29A falsely suggests apparent monophyly of the Clausilioidea and Oreohelicidae, which belong in fact to the Acavoidea although still having some more plesiomorphic characters than the other families belonging to the latter. The Oreohelicidae are then Gondwanian in origin, and reached North America before the end of the Mesozoic. The clausilioid families have either followed the same track to the northern continents and back to the Gondwanian regions, or represent a Pangean group of which the Megaspiridae are the Gondwanian relict whereas the other families represent a radiation issuing from the Northern Hemisphere. This last solution involves one migration fewer than the others, and results in the tree shown Text-fig. 29B. The consequence of this tree is acceptance of the idea that the two non-orthurethran suborders were already differentiated during the Carboniferous, even though no element allows construction of a scenario for this divergence.

The date of the divergence of the Endodontidea and Acavoidea can hardly be estimated because the superfamilies are not vicariant; however, it is doubtless anterior to the breakup of Gondwana. The patterns of the various families have been discussed above.

The Dolichonephra contains the Helicoidea, Achatinoidea and Zonitoidea. The similarity of the shell of the Carboniferous genus *Protodiscus* to the shell of the zonitoid Discidae is consistent with both the position of the Zonitoidea on the tree shown in Text-fig. 29B, and the hypothesis of the differentiation of the suborders before the break-up of Pangea.

The position of the Achatinoidea as the sister group of the Helicoidea fits the hypothesis of their Laurasian origin better than the hypothesis of their Gondwanian origin discussed above (the synapomorphy that allows the distinction of the Achatinoidea from the Helicoidea is the primary absence of an amatorial organ, not taken into account in Appendix G).

There are surprisingly few elements indicating an origin of the familial and suprafamilial groups of the Stylommatophora through vicariance events. The suborders might be originally vicariant only if: either all the Clausilioidea are of Gondwanian origin, a hypothesis that contradicts Pilsbry's hypotheses (1904) and implies more migrations and extinctions than does the hypothesis of the differentiation of suborders anterior to the break-up of Pangea; or the suborders originated before the formation of Pangea. In addition, there is no pair of superfamilies of which the vicariant origin can be recognized. Finally, within the superfamilies there are few pairs of families or family groups whose origin is probably vicariant: clausilioid groups of families; Partulidae—Enidae; Endodontidae—Systrophiidae—Punctidae + Athoracophoridae; possibly Helicidae—Helminthoglyptidae, insofar as both are monophyletic.

On the contrary, there are many indications of migrations, as shown in the discussions of the history of the various superfamilies: the general impression is that most usually the sister groups diverged within a biogeographic region, and that the present geographic distributions result from subsequent dispersals (e.g. Subulinidae and Streptaxidae). However, this general impression should not be considered definitive for two reasons. First is the scarcity of fossils and the difficulties of assigning them to a family (convergence and symplesiomorphy in shell characters); in particular the quasi-absence of fossils older than Danian is dramatic, because most Recent superfamilies seem to be older. Second is the imprecision of paleogeographical data for older periods, during which most families probably appeared: the incertitudes about the place and date of the appearance of the various groups forbids us to exclude their vicariant origin in various regions of single continental units. It might be more reliable to revise the families and try to propose phylogenies for genera. Unfortunately, both collections (it seems, for example, that no museum has preserved Megaspiridae) and systematists are lacking.

CLASSIFICATION

In the classification which follows, the superfamilies seem large compared with those proposed by Solem (1978) or Boss (1982). I do not believe it very important, the only real problem being to recognize monophyletic units; furthermore, nothing keeps one from using more restricted groups at suprafamilial rank. Fifty-one families being classified in three suborders, the information would be maximal if every suborder included 17 families and four superfamilies of about four families each. The classification presented below is not very far from these numbers, although not deliberately so. The two superfamilies that might seem very large compared with the other ones, i.e. the Helicoidea and Zonitoidea, are precisely those whose phylogeny I consider the most poorly resolved. The classification of the Orthurethra is not very satisfying, as noted above, more especially as the Chondrinoidea are polyphyletic according to my hypotheses; however, my feeling is that it is worth recognizing the Partuloidea, whereas I am not very confident of the position of the Chondrinidae in the tree of Text-fig. 22.

- Order Stylommatophora
  - Suborder Orthurethra
    - Superfamily Pupilloidea
      - Valloniidae (+ Strobilopsidae)
      - Achatinellidae (+ Tornatellinidae)
      - Pupillidae
      - Pyramidulidae
    - Superfamily Chondrinoidea
      - Chondrinidae
      - Vertiginidae
      - Orculidae
      - Cochlicopidae
      - Amastridae
    - Superfamily Partuloidea
      - Partulidae
      - Enidae
  - Suborder Dolichonephra
    - Superfamily Zonitoidea
      - Zonitidae
      - Trochomorphidae
      - Euconulidae
      - Discidae
      - Arionidae (+ Philomycidae)
      - Parmacellidae
      - Limacidae
      - Milacidae

        Trigonochlamydidae
    Superfamily Helicoidea
        Helicidae
        Helminthoglyptidae
        Bradybaenidae
        Polygyridae
        Camaenidae
        Sagdidae
        Haplotrematidae
        Helicarionidae (+ Aillyidae)
        Vitrinidae
    Superfamily Achatinoidea
        Achatinidae
        Subulinidae
        Streptaxidae
        Oleacinidae(+Spiraxidae,Testacellidae)
        Ferussaciidae
        Succineidae
Suborder Brachynephra
    Superfamily Clausilioidea
        Megaspiridae
        Clausiliidae
        Cerionidae
        Urocoptidae
        Bulimulidae
    Superfamily Endodontoidea
        Charopidae
        Endodontidae
        Systrophiidae
        Punctidae
        Athoracophoridae
    Superfamily Acavoidea
        Oreohelicidae (+ Ammonitellidae)
        Corillidae
        Acavidae
        Rhytididae (+ Chlamydephoridae)

CONCLUSIONS

The goal of the first part of this work is primarily to describe hitherto unknown morphologies and their variations within the stylommatophoran plan of organization in relation to classification; it is also an attempt to identify and eliminate the characters obviously functional or redundantly variable. Although the practical result is original, the principle is not: as noted by Cain (1982), nearly every systematist (but not he) tries to use non-adaptive characters to build classifications. If reached, this objective implies that *taxonomic* diversity does not result from adaptation: if applied to groups that are defined by non-adaptive characters, the concept of adaptive radiation is at least ambiguous. As discussed elsewhere (Tillier, 1986), the contradiction between the adaptationist program and elaboration of phylogenetic classification can be shown as follows: first, characters are adaptive; second, if adaptive characters are used to build classifications, selection pressures will be classified instead of kinships; third, therefore non-adaptive characters should be used to build phylogenetic classifications; fourth, go to step one. The obligation to use non-adaptive characters to build phylogenetic classifications implies that macroevolution is neutral regarding adaptation. The tenet that all evolution results from adaptation, defended by the neo-Darwinians, should result in renunciation of phylogenetic reconstruction and therefore in a modification of taxonomic principles and of the theories of biological classifications, at present based on the principle of a relationship between kinship and classification.

There is no doubt that the classification presented above is very far from perfect. However, I believe it at least as coherent as those presented by Solem (1978) and Boss (1982). Insofar as it represents progress, this lies in the set purpose of elaborating a phylogenetic classification, and hopefully in the possibility for the reader of finding the reasons for taxonomic decisions without having to reexamine all the materials I have dissected.

Of course the necessity of attempting to build a phylogenetic classification of land snails and slugs can be questioned, inasmuch as the basically phenetic classifications of the Pilsbry-Baker type have recently raised no other protest than Schileyko's (1978a, b), whose results are, in my opinion, far from convincing (problem of translation?). The principal inconvenience of classifications built on a phenetic basis is that their control is not possible without wide personal experience; but there is no doubt that to some extent they allow generalizations and predictions on morphological characters. Imperfect as it might appear, a phylogenetic classification seems better to me for two reasons. First, it is better to try to provide an image of the history of the group that is unique and independent of the observer, than an image of similarities which necessarily depend on the observer. Secondly, if evolution is the efficient cause of the apparent order of the living, kinship is the formal cause. If one is interested mainly in evolutionary mechanisms, one will give precedence to the efficient causes in building classifications and, as I tried to discuss, will favor morphological similarity in relation to the current theory of evolution. Favoring formal causes, as attempted by the phylogenetic systematicist, seems better to me, inasmuch as a classification should be a plan of the natural order, not an account of the realization of this plan. In both cases it is easy to pass to the final causes, the evocation of which provokes repugnance in contemporary biologists, and it should be kept in mind that the word adaptation is finalist not only in etymology, but also in usage: talking about adaptation to an environment, instead of talking about adaptation to a biological property under the action of the environment, is a rather finalist expression of evolution (Gould & Lewontin, 1979; Gould & Vrba, 1982). However, the synthetic theory doubtless better prevents finalism than the absence of macroevolutionary theory.

The dilemma between phenetics and phylogenetics was avoidable as long as it was believed that homoplasy is exceptional, and as the absence of phylogenetic significance of symplesiomorphy was not emphasized (and as gradualism was not questioned; Tillier, 1986). Unfortunately, for this approach had the immense merit of being simple, the application of the methods and principles of Hennig (1966) revealed more homoplasies than anyone expected, and the importance of this problem seems to be *de facto* avoided by most phylogeneticists (Cain, 1982, 1983). The abundance of parallel evolution evident in the Stylommatophora, associated with the larger number of taxa under study, obliged me to use minimization of phyletic distances as a criterion of choice for phyletic relationships. I can justify this approach only by a postulate following which the appearance of a given character state in two taxa is more probable when these taxa are phylogenetically closer. This postulate is not justified in the synthetic theory of evolution, but it seems to me that it is implicit in all methods of phylogenetic reconstruction in which minimization is used. In addition, accepting the generality of homoplasy implies a shift in the meaning of the word "synapomorphy" from its restricted sense, i.e. "uniquely derived character state," to its etymological sense, i.e. "derived character state uniting taxa."

The classification so constructed and proposed above should be both tested and improved. Three areas in particular require attention. First, the sampling should be improved. The method used here necessitates using the most plesiomorphic state occurring in each taxon classified. In most cases, my sampling is such that correspondence between what has been done and this intention would be pure chance; in particular the sample should be extended in the Orthurethra and most families of which few species have been examined, not to mention the Megaspiridae, the only important family of which no specimen was available. Secondly, characters of the hard parts might be added. Although it might be expected that shell and radular morphology converge too easily to be really useful at high taxonomical levels, Solem (1983; Solem & Yochelson, 1979) showed at least similarities in microscopical structures that might have some taxonomic value; the problem is to determine at which taxonomic level these characters vary, and to determine the direction of their evolution. Thirdly, characters of the genital system might be included. At present it does not seem possible to determine which genital characters can be used to determine relationships among families and at higher taxonomic levels, a few cases excepted. A plethora of opinions can be found, but, as far as I know, no verification based upon comparable and numerous enough elements. Cain (1982, 1983) has proposed the use of secondary sexual characters in phylogenetic reconstruction, in particular in pulmonate gastropods, for theoretical reasons. This approach has not been attempted here because I preferred to describe and compare first other organ systems far less known in order to make them usable, but it is worth being tried.

In general conclusion, one cannot insist strongly enough on the necessity for a real theory of macroevolution, which does not now exist. I hope to have shown here and elsewhere (Tillier, 1986), perhaps too briefly, that the approach adopted above, although classical in principle, requires hypotheses that current theory about evolutionary mechanisms does not justify. The synthetic theory has allowed immense progress in species and population taxonomy, but we still await the theory that will allow equivalent progress at the generic level and above.

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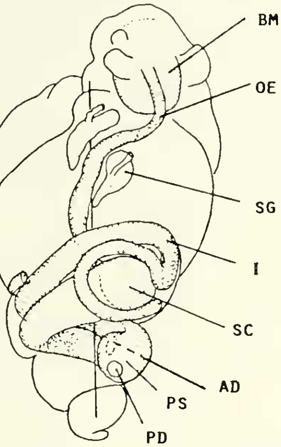
ABBREVIATIONS

A	anus
AD	anterior duct of digestive gland
AG	albumen gland
AO	aorta
AS	stomachal appendix
AU	auricle
BM	buccal mass
BP	pallial border
C	crop
CC	cerebral commissure
CG	cerebral ganglion
CJ	conjunctive tissue
DC	diverticulum of duct of digestive gland
DS	diverticulum of gastric pouch
GP	pallial gland
GU	ureteric groove
HD	hermaphrodite duct
HG	hermaphrodite gland
I	intestine
K	kidney
KO	kidney pore
LOP	pallial lobe
NO	optic nerve
OC	oesophageal crop
OE	oesophagus
OR	ocular retractor muscle
P	penis
PAD	right parietal ganglion
PAG	left parietal ganglion
PD	posterior duct of digestive gland
PG	pedal ganglion
PGL	pedal gland
PLD	right pleural ganglion
PLG	left pleural ganglion
PN	pneumostome
PO	reno-pericardial pore
PR	penial retractor muscle
PS	gastric pouch
R	rectum
RM	retractor muscle
RS	radular sheath
SC	gastric crop
SG	salivary gland
SO	spermoviduct
SP	spermatheca
STA	statocyst
TD	digestive tract
TG	genital apparatus
TY	typhlosole
U	ureter
UA	ureteric appendix
UO	ureteric pore
VA	vagina
VD	vas deferens
V	ventricle
VG	visceral ganglion

FIGS. 1–10: ACHATINELLIDAE. *Nota bene:* the scale line in each plate varies in value; the length stated in an individual caption is the length of the scale line with respect to that figure.
1) *Auriculella auricula,* digestive tract. 4mm.
2) *Auriculella auricula,* nervous system in dorsal view. 2mm.
3) *Idem,* cerebral commissure cut. 2mm.
4) *Elasmias* sp., nervous system in dorsal view, cerebral commissure cut. 1mm.
5) *Elasmias* sp., pulmonary complex. 2mm.
6) *Elasmias* sp., kidney internal morphology. 2mm.
7) *Lamellidea* cf. *pusilla,* digestive tract. 2mm.
8) *Lamellidea* cf. *pusilla,* nervous system in dorsal view. 1mm.
9) *Idem,* cerebral commissure cut. 1mm.
10) *Elasmias* sp., digestive tract. 2mm.

1



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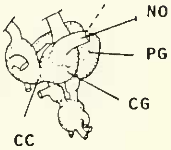

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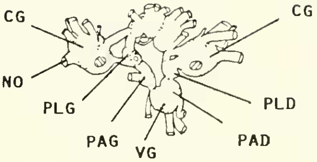

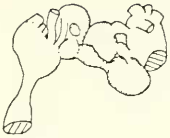

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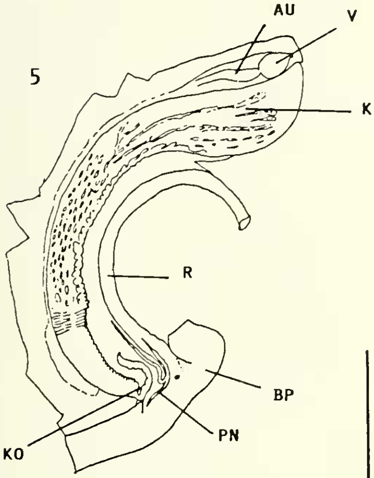

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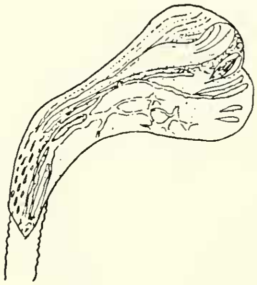

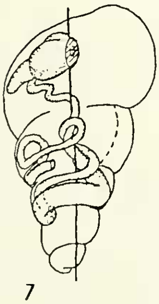

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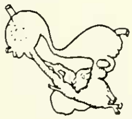

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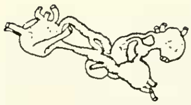

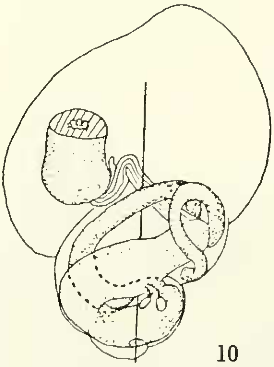

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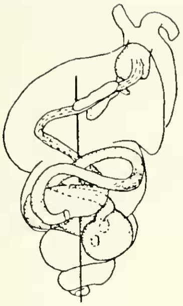
FIGS. 11–22: ACHATINELLIDAE
11) *Tornatellides oblongus*, digestive tract. 2mm.
12) *Strobilus plicosa*, digestive tract. 2mm.
13) *Tekoulina pricei*, digestive tract. 4mm.
14) *Tornatellides oblongus*, nervous system in dorsal view. 1mm.
15) *Idem*, cerebral commissure cut. 1mm.
16) *Achatinella lorata*, digestive tract. 8mm.
17) *Strobilus plicosa*, nervous system in dorsal view. 1mm.
18) *Idem*, cerebral commissure cut. 1mm.
19) *Tekoulina pricei*, nervous system in dorsal view. 1mm.
20) *Idem*, cerebral commissure cut. 1mm.
21) *Achatinella lorata*, nervous system in dorsal view. 2mm.
22) *Idem*, cerebral commissure cut. 2mm.

11



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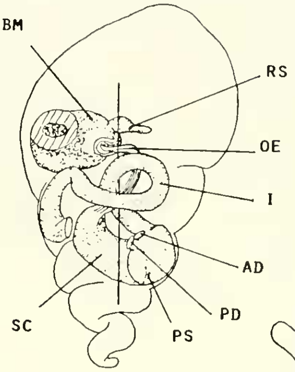

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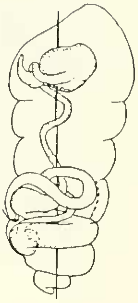

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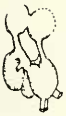

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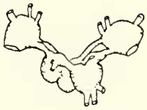

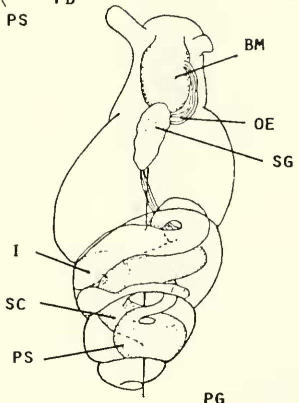

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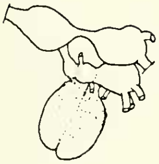

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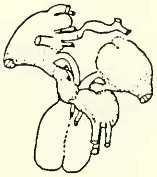

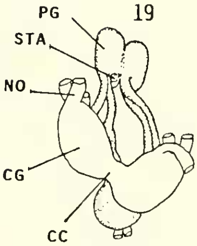

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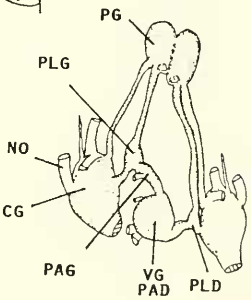

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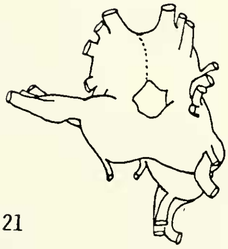

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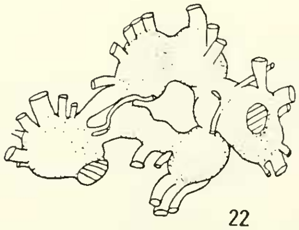

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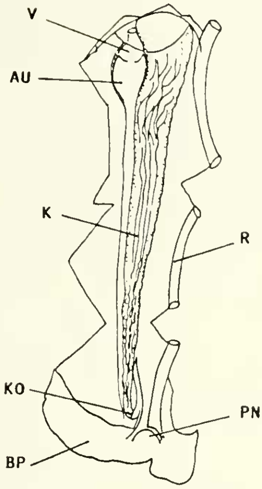
FIGS. 23–28: ACHATINELLIDAE, PARTULIDAE
23) *Achatinella lorata*, pulmonary complex. 8mm.
24) *Achatinella lorata*, kidney internal morphology. 4mm.
25) *Eua expansa*, internal morphology of gastric pouch. 2mm.
26) *Eua expansa*, digestive tract. 8mm.
27) *Eua expansa*, nervous system in dorsal view. 2mm.
28) *Idem*, cerebral commissure cut. 2mm.

23



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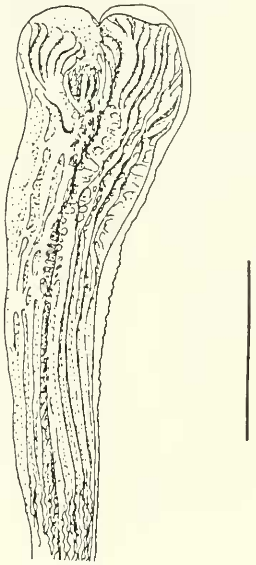

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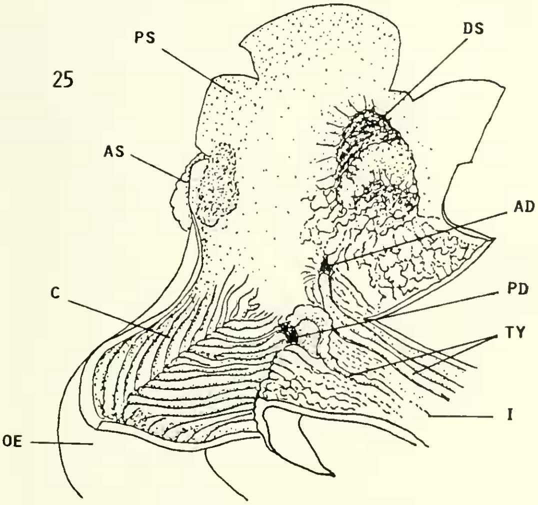

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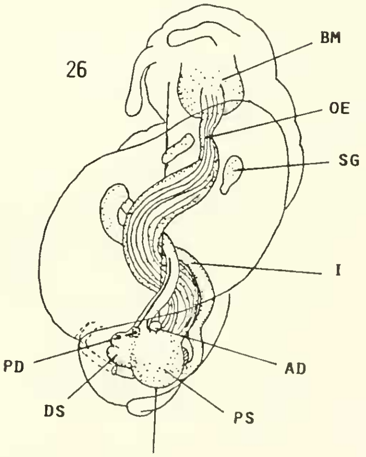

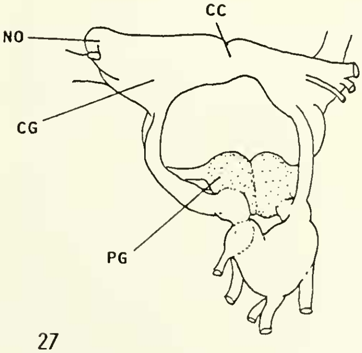

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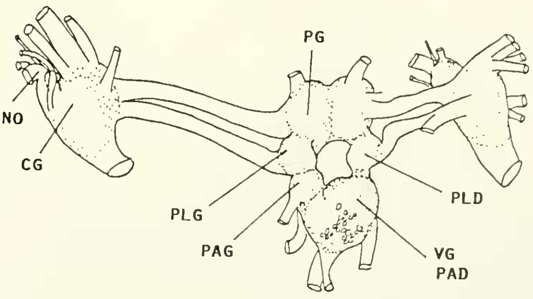

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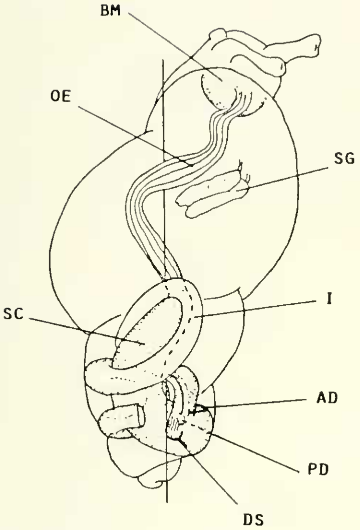
FIGS. 29–35: PARTULIDAE, AMASTRIDAE
29) *Partula caledonica,* digestive tract. 7mm.
30) *Partula caledonica,* kidney internal morphology. 4mm.
31) *Idem,* external morphology. 7mm.
32) *Partula caledonica,* nervous system in dorsal view. 2mm.
33) *Idem,* cerebral commissure cut. 2mm.
34) *Amastra pullata,* nervous system in dorsal view. 2mm.
35) *Idem,* cerebral commissure cut. 2mm.

29



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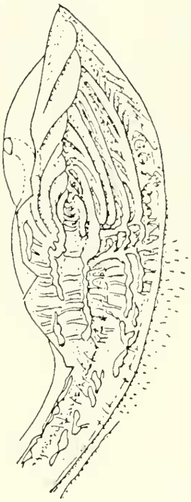

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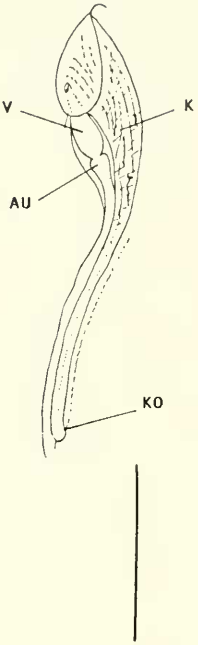

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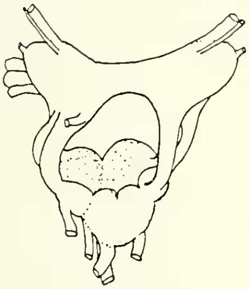

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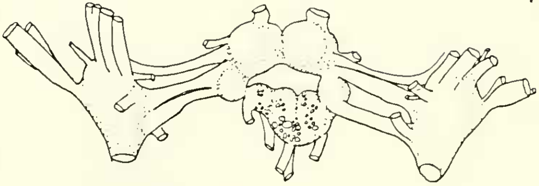

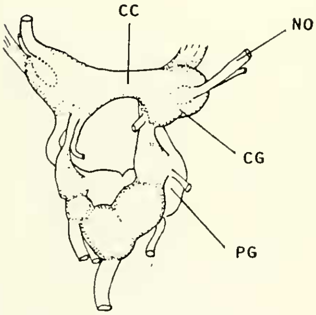

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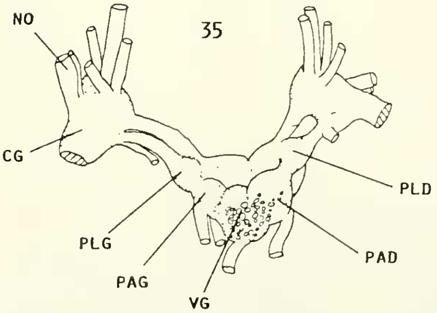
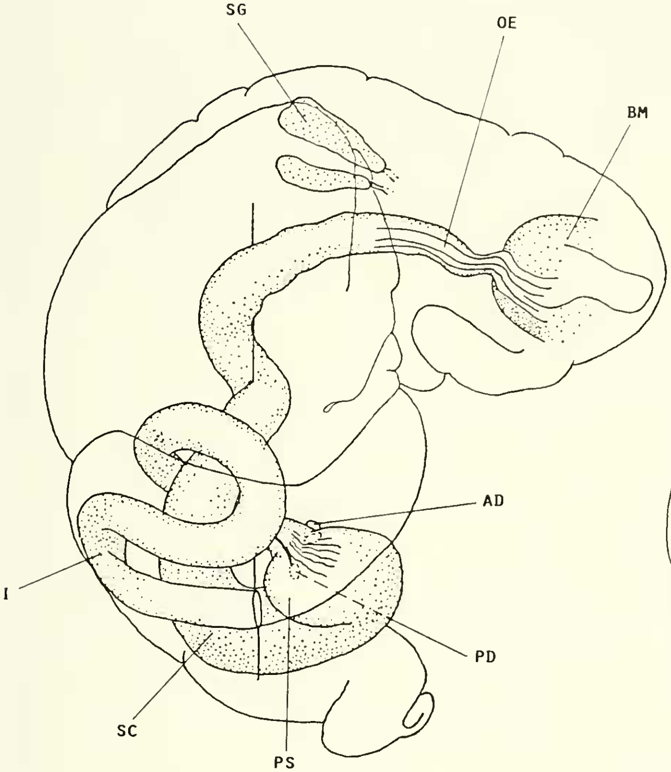


FIGS. 36–42: AMASTRIDAE
36) *Amastra pullata*, digestive tract. 4mm.
37) *Amastra pullata*, morphology of gastric region. 3.8mm.
38) *Leptachatina balteata*, digestive tract. 3.8mm.
39) *Leptachatina balteata*, pulmonary complex. 7.6mm.
40) *Leptachatina balteata*, kidney internal morphology. 4mm.
41) *Leptachatina balteata*, nervous system in dorsal view. 1mm.
42) *Idem*, cerebral commissure cut. 1mm.

36



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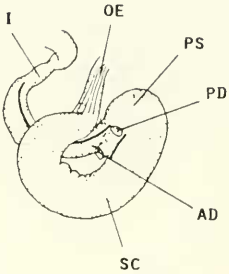

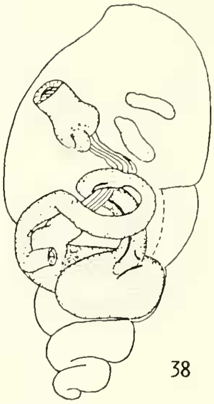

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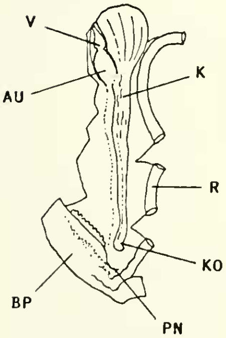

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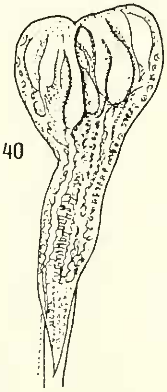

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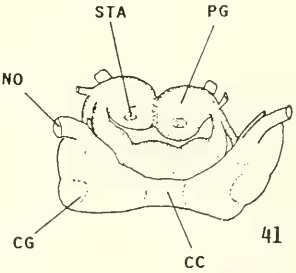

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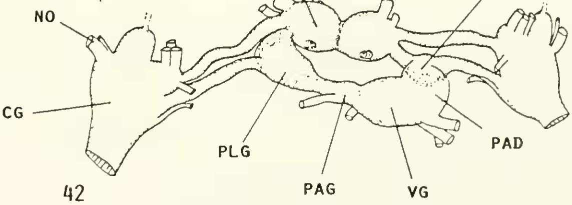

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FIGS. 43–51: COCHLICOPIDAE, PYRAMIDULIDAE
43) *Cochlicopa lubrica*, digestive tract. 4mm.
44) *Cochlicopa lubrica*, pulmonary complex. 4mm.
45) *Cochlicopa lubrica*, kidney internal morphology. 2mm.
46) *Pyramidula rupestris*, nervous system in dorsal view. 0.5mm.
47) *Cochlicopa lubrica*, nervous system in dorsal view. 1mm.
48) *Idem*, cerebral commissure cut. 1mm.
49) *Pyramidula rupestris*, digestive tract. 0.9mm.
50) *Pyramidula rupestris*, pulmonary complex. 1.9mm.
51) *Pyramidula rupestris*, kidney internal morphology. 1mm.

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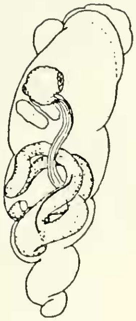

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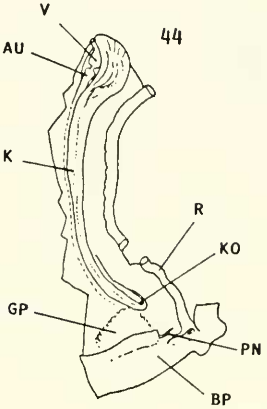

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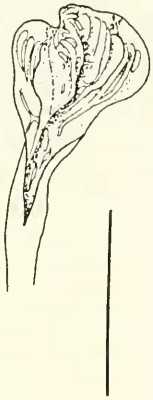

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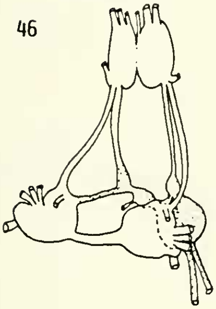

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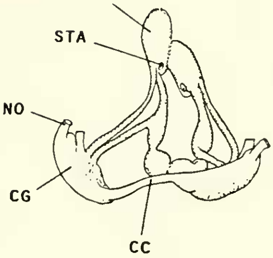

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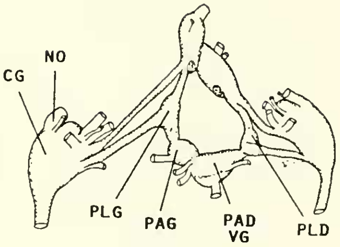

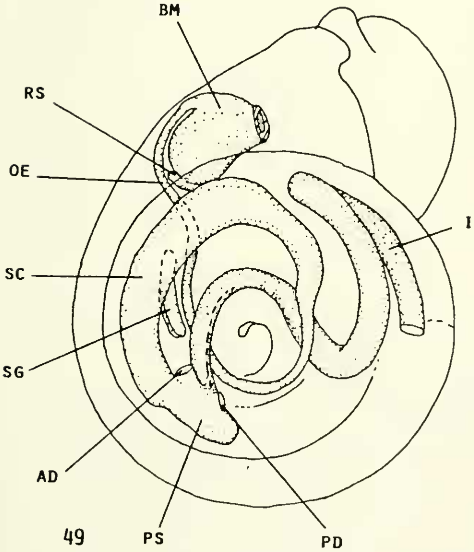

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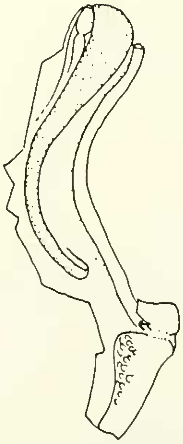

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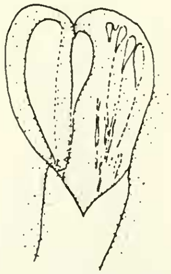
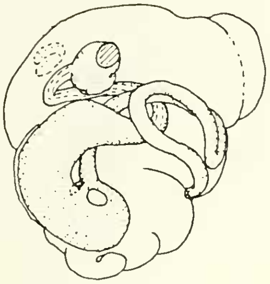


51

FIGS. 52–64: VERTIGINIDAE, ORCULIDAE
52) *Bothriopupa breviconus,* digestive tract. 1mm.
53) *Bothriopupa breviconus,* nervous system in dorsal view. 1mm.
54) *Idem,* cerebral commissure cut. 1mm.
55) *Sterkia eyriesii,* digestive tract. 1mm.
56) *Pagodulina serveri,* digestive tract. 2mm.
57) *Pagodulina serveri,* pulmonary complex. 3mm.
58) *Orcula dolium,* pulmonary complex. 4.3mm.
59) *Orcula dolium,* kidney internal morphology. 2.5mm.
60) *Orcula dolium,* digestive tract. 2.9mm.
61) *Pagodulina serveri,* nervous system in dorsal view. 1.3mm.
62) *Idem.* cerebral commissure cut. 1.3mm.
63) *Orcula dolium,* nervous system in dorsal view. 1.25mm.
64) *Idem.* cerebral commissure cut. 1.25mm.

52



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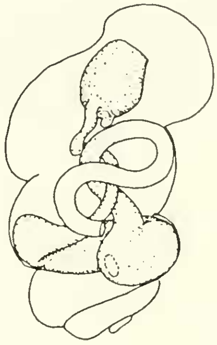

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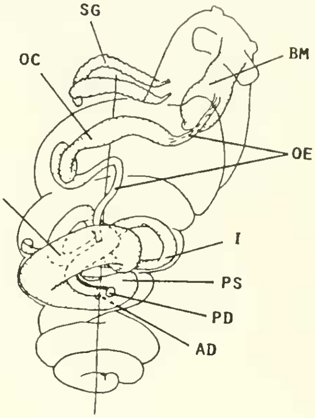

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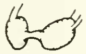

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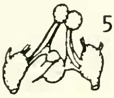

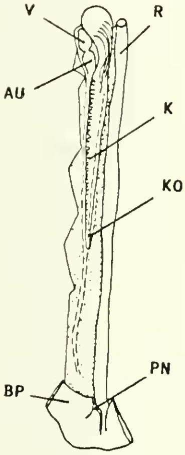

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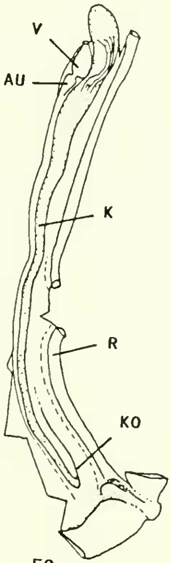

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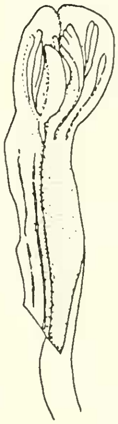

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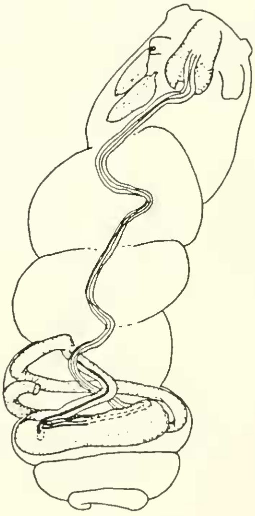

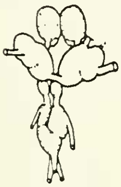

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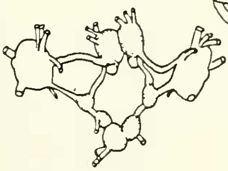

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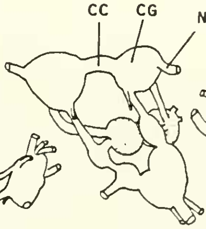

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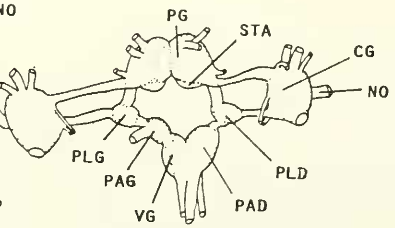
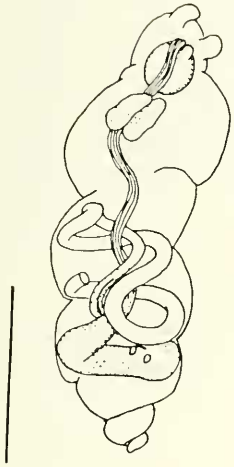


64

FIGS. 65–73: CHONDRINIDAE
65) *Solatopupa similis*, digestive tract. 2.6mm.
66) *Solatopupa similis*, pulmonary complex. 2.8mm.
67) *Solatopupa similis*, kidney internal morphology. 2mm.
68) *Solatopupa similis*, morphology of gastric region. 2mm.
69) *Solatopupa similis*, nervous system in dorsal view. 1mm.
70) *Idem*, cerebral commissure cut. 1mm.
71) *Gyliotrachela depressispira*, digestive tract. 1mm.
72) *Gyliotrachela depressispira*, nervous system in dorsal view. 0.5mm.
73) *Idem*, cerebral commissure cut. 0.5mm.

65



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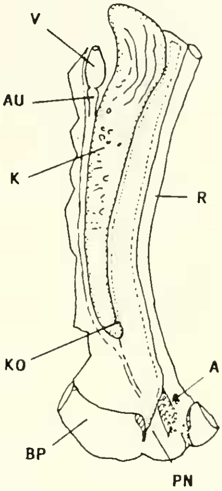

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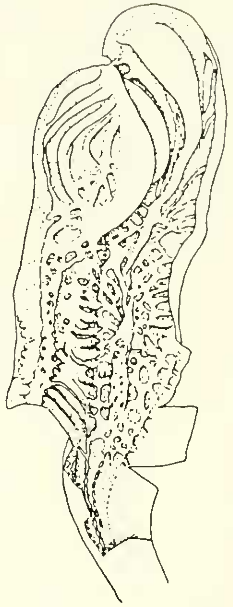

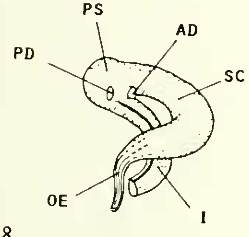

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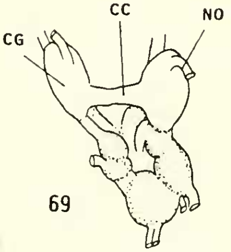

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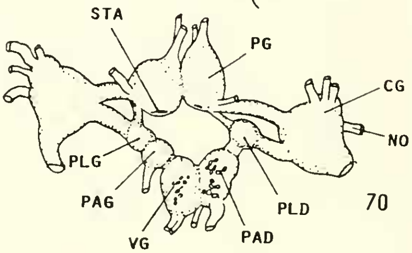

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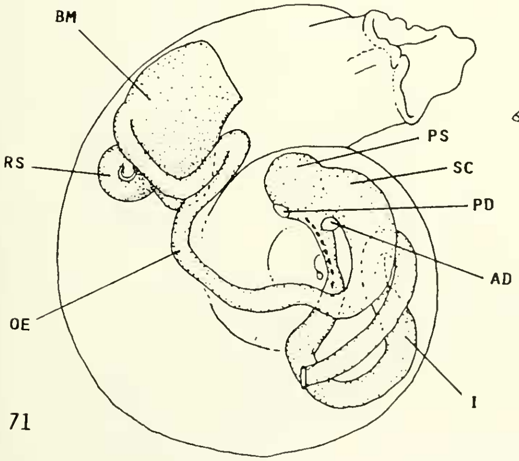

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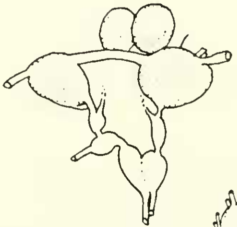

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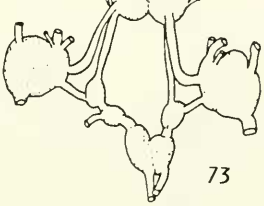
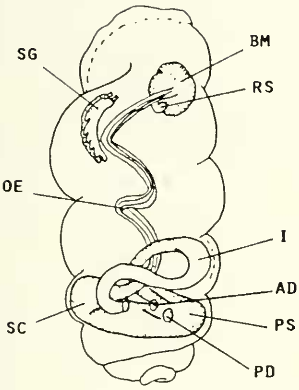


73

FIGS. 74–85: PUPILLIDAE, VALLONIIDAE
74) *Pupilla muscorum*, digestive tract. 2mm.
75) *Pupilla muscorum*, pulmonary complex. 2mm.
76) *Pupilla muscorum*, kidney internal morphology. 2mm.
77) *Lauria cylindracea*, nervous system in dorsal view. 1.2mm.
78) *Idem*, cerebral commissure cut. 1.2mm.
79) *Pupilla muscorum*, nervous system in dorsal view. 1mm.
80) *Idem*, cerebral commissure cut. 1mm.
81) *Lauria cylindracea*, digestive tract. 2mm.
82) *Pupilla muscorum*, morphology of gastric region. 2mm.
83) *Lauria cylindracea*, morphology of gastric region. 2mm.
84) *Vallonia albula*, digestive tract. 1mm.
85) *Vallonia albula*, nervous system in dorsal view, cerebral commissure cut. 1mm.

74



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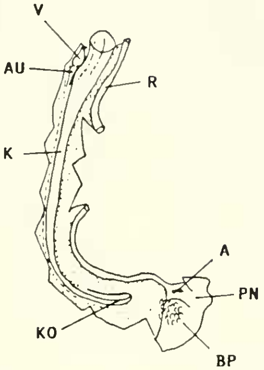

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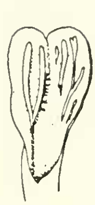

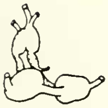

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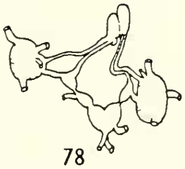

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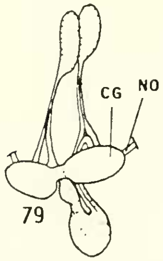

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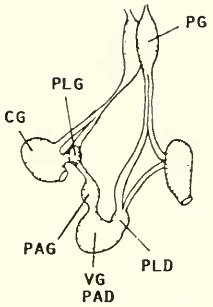

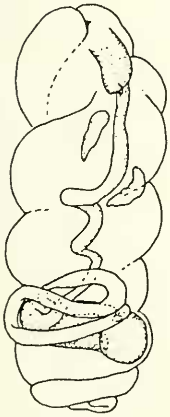

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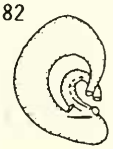

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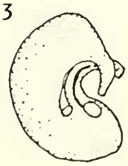

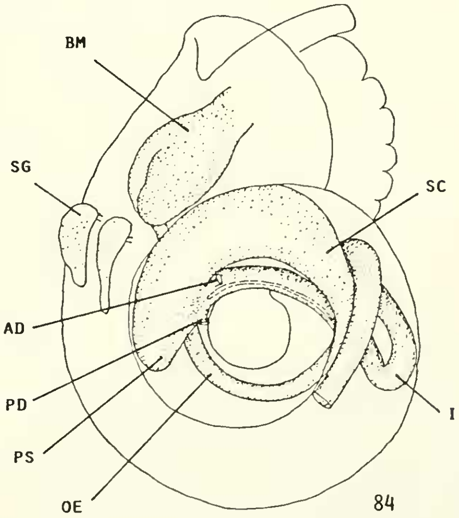

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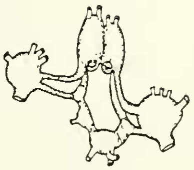
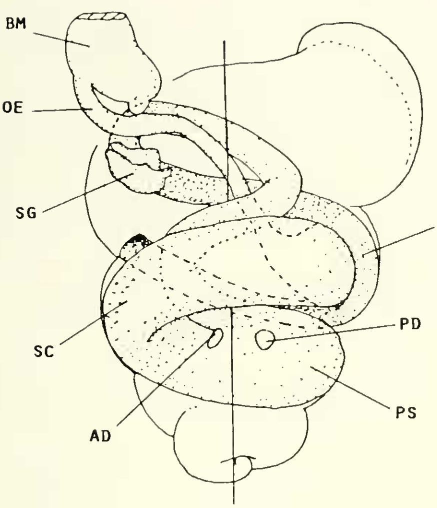


85

FIGS. 86–94: VALLONIIDAE
86) *Acanthinula aculeata,* digestive tract. 1mm.
87) *Acanthinula aculeata*, pulmonary complex. 1mm.
88) *Acanthinula aculeata*, nervous system in dorsal view. 1mm.
89) *Idem*, cerebral commissure cut. 1mm.
90) *Ptychopatula dioscoricola*, digestive tract. 1mm.
91) *Ptychopatula dioscoricola*, pulmonary complex. 1.8mm.
92) *Ptychopatula dioscoricola*, kidney internal morphology. 1.125mm.
93) *Ptychopatula dioscoricola*, nervous system in dorsal view, cerebral commissure cut. 0.6mm.
94) *Ptychopatula dioscoricola*, nervous system in dorsal view. 0.6mm.

86



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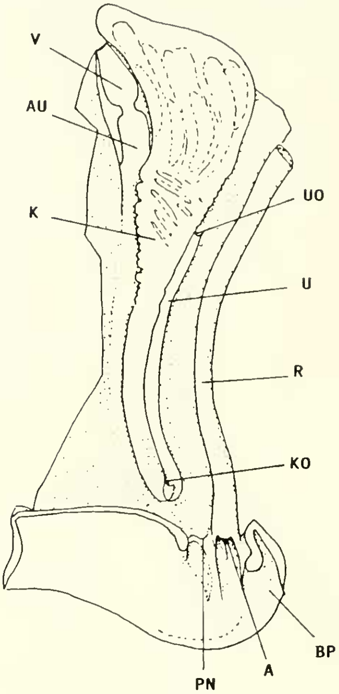

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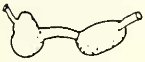

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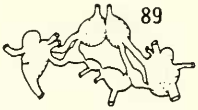

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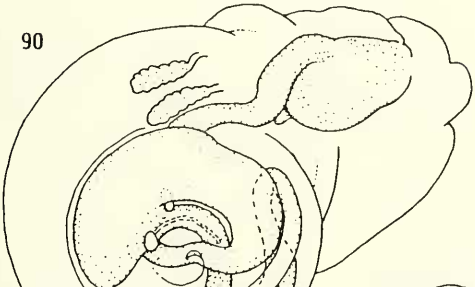

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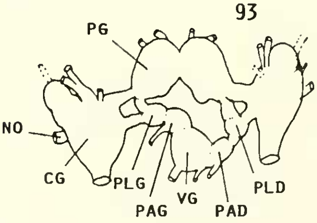

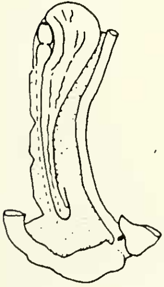

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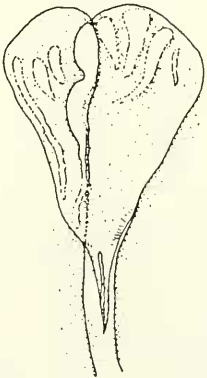

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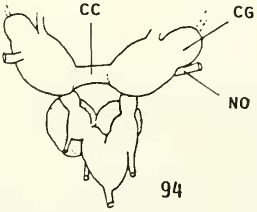

94

FIGS. 95–104: VALLONIIDAE
95) *Spermodea lamellata*, digestive tract. 1mm.
96) *Spermodea lamellata*, nervous system in right lateral view. 1mm.
97) *Spermodea lamellata*, nervous system in dorsal view, cerebral commissure cut. 1mm.
98) *Strobilops aenea*, pulmonary complex. 1mm.
99) *Strobilops aenea*, kidney internal morphology. 1mm.
100) *Spermodea lamellata*, pulmonary complex. 1.9mm.
101) *Spermodea lamellata*, kidney internal morphology. 1mm.
102) *Strobilops aenea*, nervous system in dorsal view. 0.54mm.
103) *Idem*, cerebral commissure cut. 0.54mm.
104) *Strobilops aenea*, digestive tract. 1mm.

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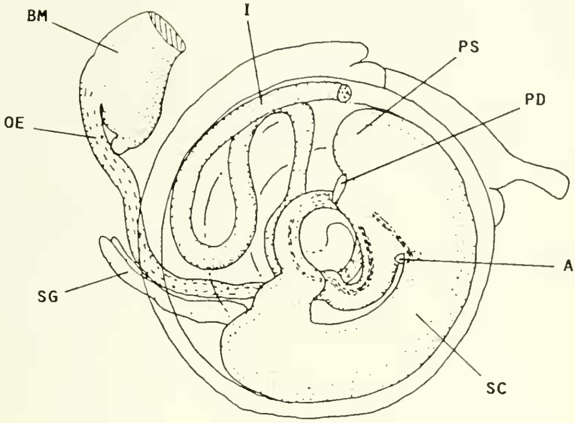

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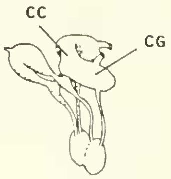

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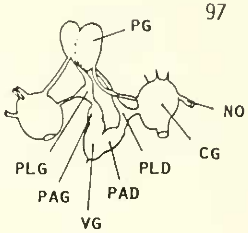

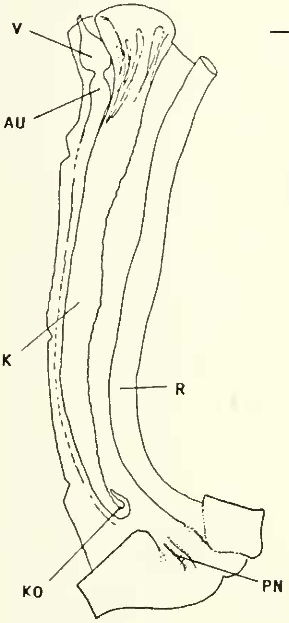

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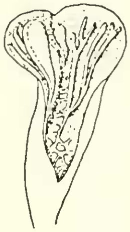

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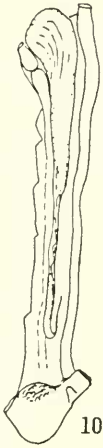

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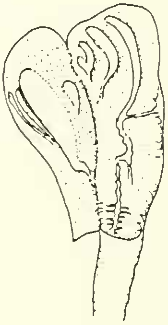

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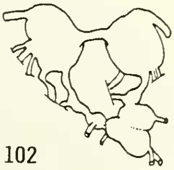

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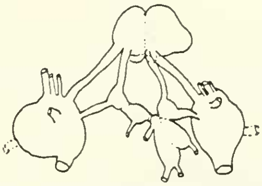

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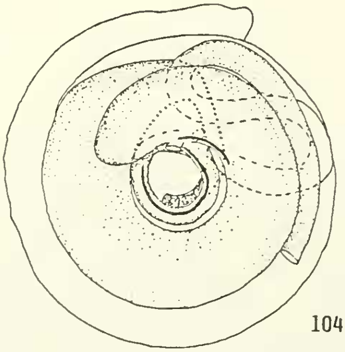

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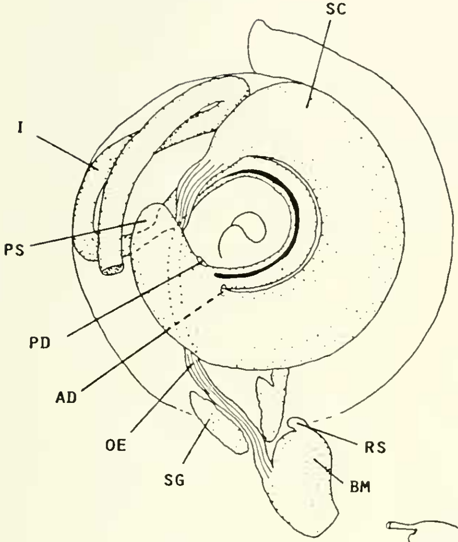
FIGS. 105–115: VALLONIIDAE, ENIDAE
105) *Klemmia magnicosta*, digestive tract. 1.6mm.
106) *Klemmia magnicosta*, pulmonary complex. 2.7mm.
107) *Klemmia magnicosta*, kidney internal morphology. 1.3mm.
108) *Chondrula tridens*, digestive tract. 4mm.
109) *Chondrula tridens*, morphology of gastric region. 3mm.
110) *Klemmia magnicosta*, nervous system in dorsal view. 1.3mm.
111) *Idem*, cerebral commissure cut. 1.3mm.
112) *Chondrula tridens*, pulmonary complex. 6.5mm.
113) *Chondrula tridens*, kidney internal morphology. 3.3mm.
114) *Chondrula tridens*, nervous system in dorsal view. 1.4mm.
115) *Idem*, cerebral commissure cut. 1.4mm.

105



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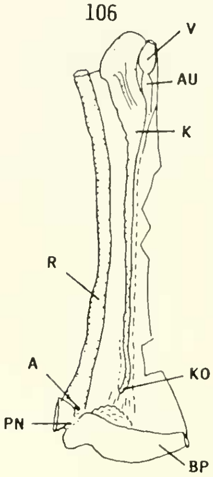

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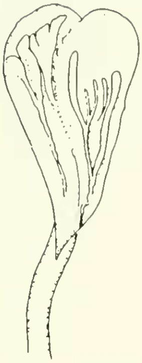

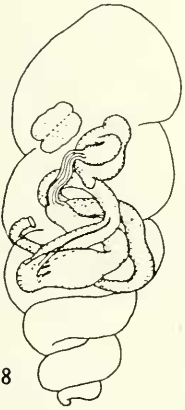

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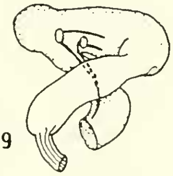

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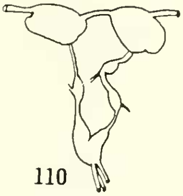

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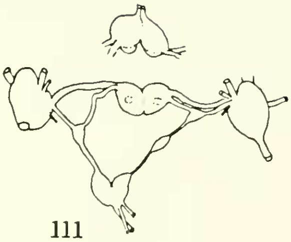

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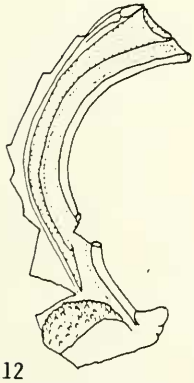

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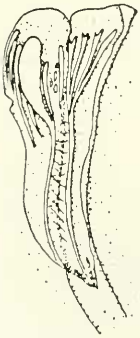

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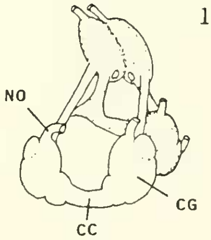
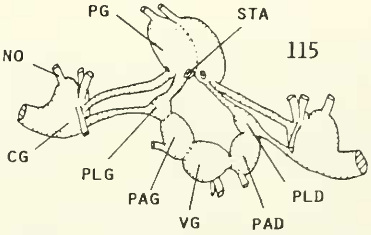
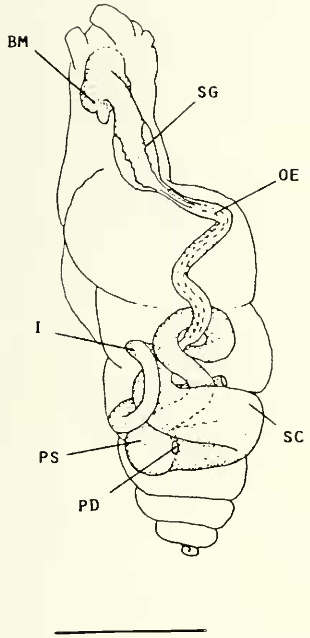




115

FIGS. 116–125: ENIDAE
116) *Imparietula jousseaumei*, digestive tract. 3.6mm.
117) *Imparietula jousseaumei*, pulmonary complex. 7.2mm.
118) *Imparietula jousseaumei*, kidney internal morphology. 3.6mm.
119) *Imparietula jousseaumei*, nervous system in dorsal view. 1.25mm.
120) *Idem*, cerebral commissure cut. 1.25mm.
121) *Zebrina detrita*, digestive tract. 7.2mm.
122) *Zebrina detrita*, pulmonary complex. 5mm.
123) *Zebrina detrita*, kidney internal morphology. 5.6mm.
124) *Zebrina detrita*, nervous system in dorsal view. 1.8mm.
125) *Idem*, cerebral commissure cut. 1.8mm.

116



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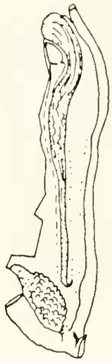

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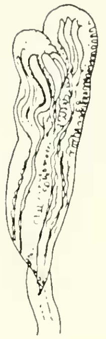

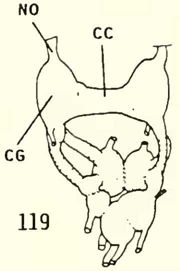

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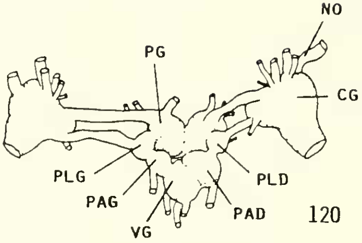

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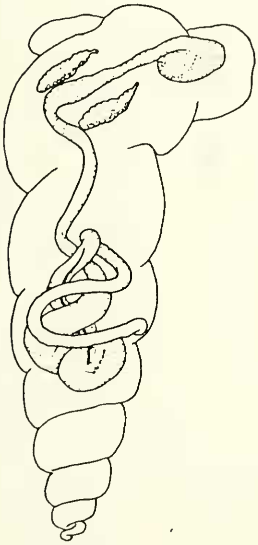

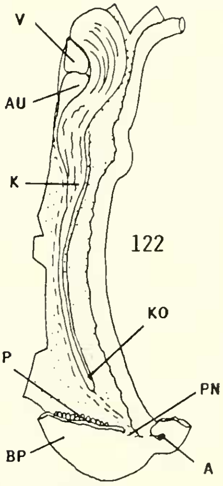

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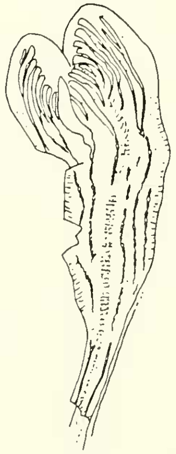

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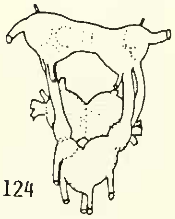

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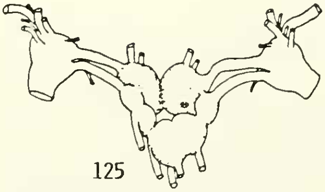
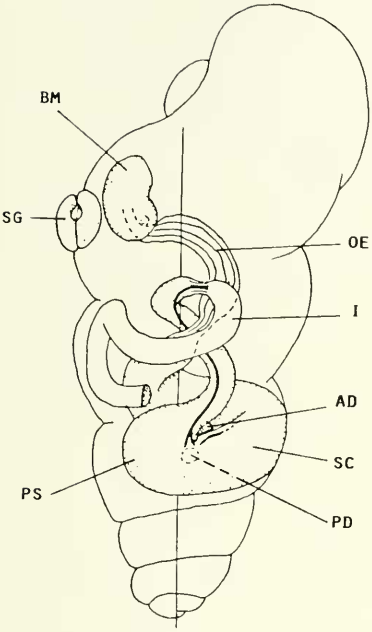


125

FIGS. 126–134: ENIDAE
126) *Ena montana*, digestive tract. 4.4mm.
127) *Ena montana*, pulmonary complex. 8.8mm.
128) *Ena montana*, kidney internal morphology. 8.8mm.
129) *Cerastua somaliensis*, digestive tract. 5.8mm.
130) *Ena montana*, nervous system in dorsal view. 1mm.
131) *Idem*, cerebral commissure cut. 1mm.
132) *Cerastua somaliensis*, nervous system in dorsal view. 2mm.
133) *Idem*, cerebral commissure cut. 2mm.
134) *Cerastua somaliensis*, pulmonary complex. 5.8mm.

126



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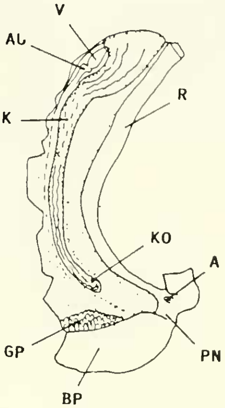

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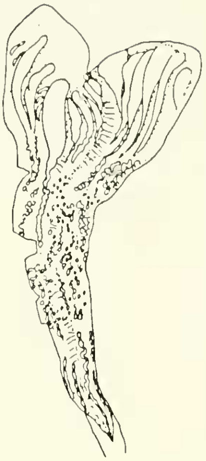

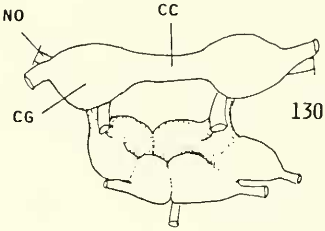

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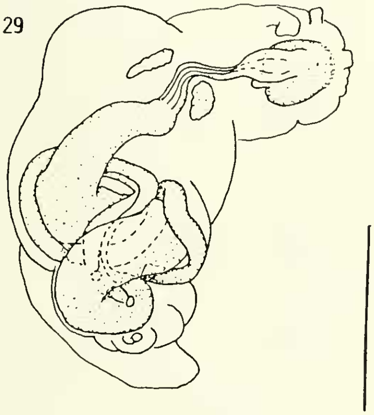

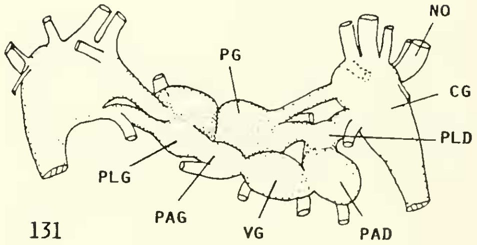

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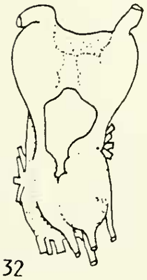

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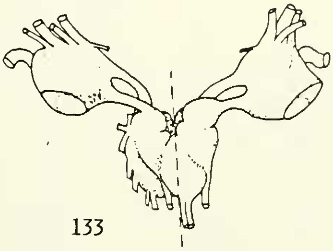

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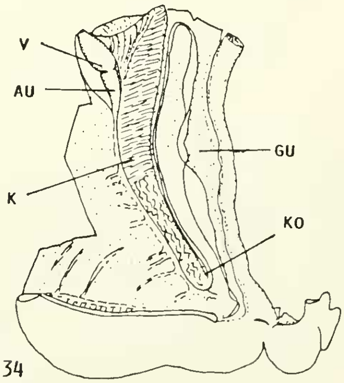
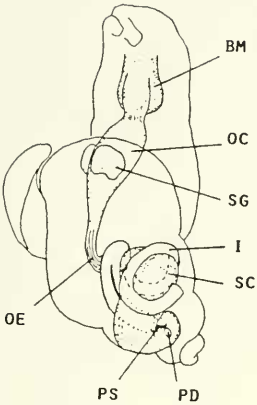


134

FIGS. 135–146: ENIDAE
135) *Rachistia histrio,* digestive tract. 9mm.
136) *Rachistia histrio,* morphology of gastric region. 9mm.
137) *Rachistia histrio,* pulmonary complex. 9mm.
138) *Rachistia histrio,* kidney internal morphology. 4.5mm.
139) *Rachistia histrio,* nervous system in dorsal view. 2mm.
140) *Idem,* cerebral commissure cut. 2mm.
141) *Draparnaudia michaudi,* pulmonary complex. 9mm.
142) *Draparnaudia michaudi,* kidney internal morphology. 4.5mm.
143) *Draparnaudia michaudi,* nervous system in dorsal view. 2mm.
144) *Idem,* cerebral commissure cut. 2mm.
145) *Amimopina macleayi,* nervous system in dorsal view. 2mm.
146) *Idem,* cerebral commissure cut. 2mm.

135



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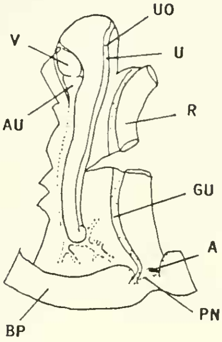

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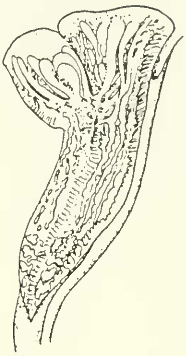

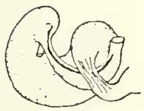

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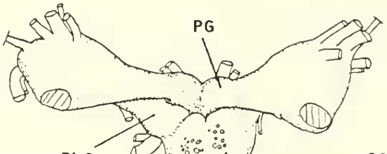

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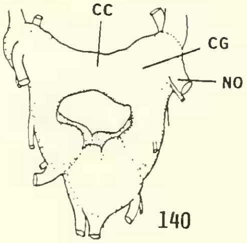

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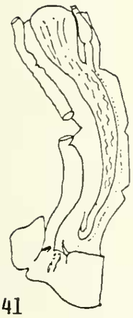

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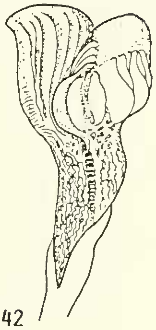

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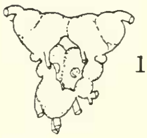

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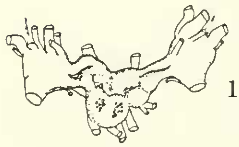

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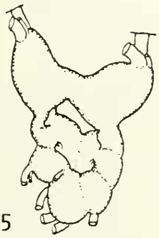

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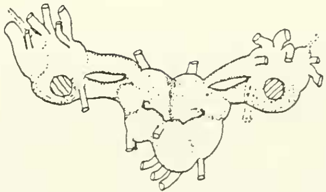
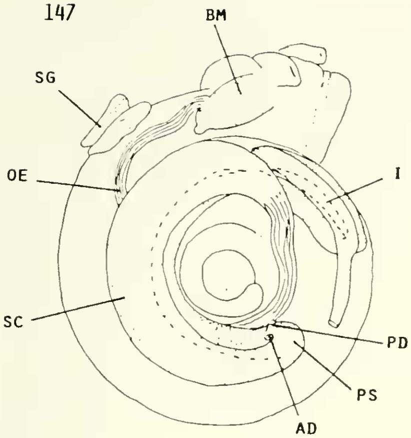


146

FIGS. 147–155: ENDODONTIDAE, CHAROPIDAE
147) *Thaumatodon hystricelloides,* digestive tract. 2mm.
148) *Thaumatodon hystricelloides,* nervous system in dorsal view. 1mm.
149) *Idem,* cerebral commissure cut. 1mm.
150) *Libera fratercula,* kidney internal morphology. 2mm.
151) *Libera fratercula,* pulmonary complex. 2mm.
152) *Libera fratercula,* digestive tract. 2.4mm.
153) *Andrefrancia* sp., nervous system in dorsal view. 1mm.
154) *Idem,* cerebral commissure cut. 1mm.
155) *Andrefrancia* sp., digestive tract. 4mm.

147



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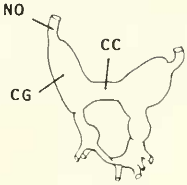

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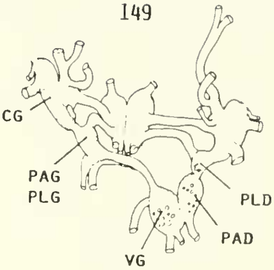

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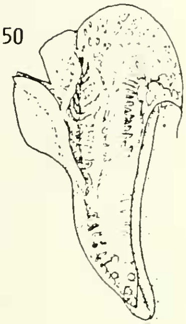

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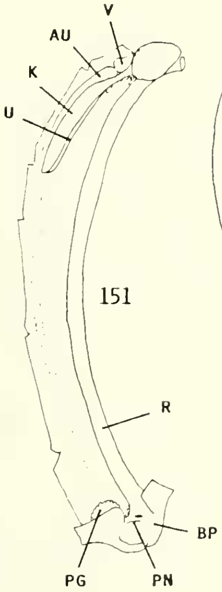

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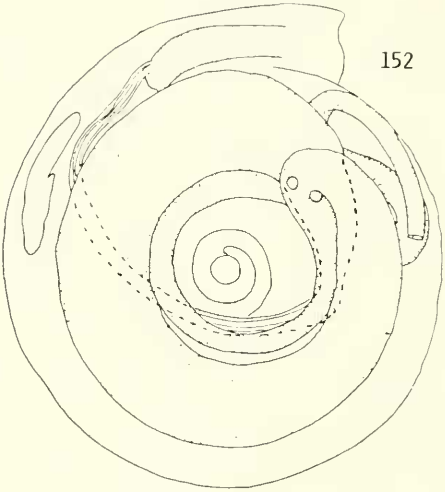

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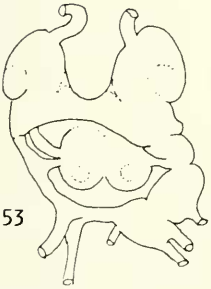

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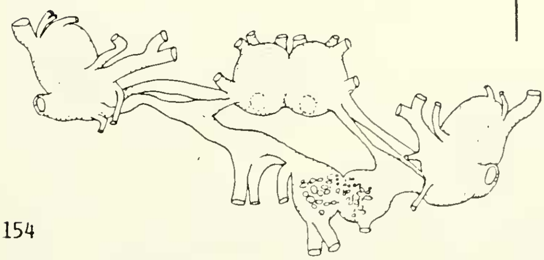

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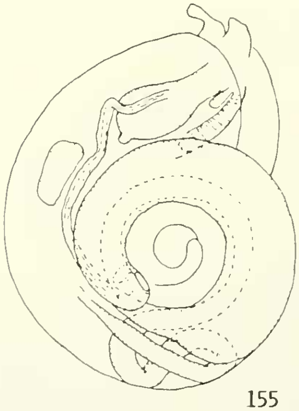
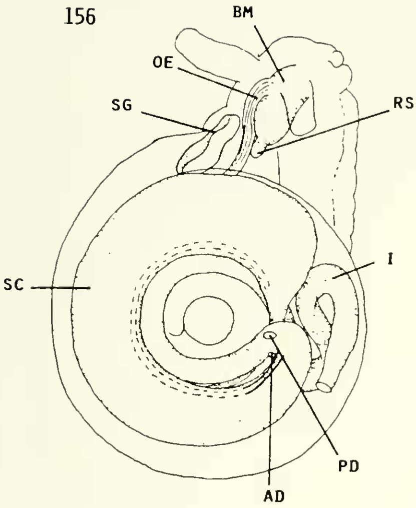


FIGS. 156–166: CHAROPIDAE
156) Charopidae sp., digestive tract. 2.25mm.
157) Charopidae sp., pulmonary complex. 4.5mm.
158) Charopidae sp., kidney internal morphology. 4.5mm.
159) *Annoselix dolosa,* digestive tract. 6.5mm.
160) *Annoselix dolosa,* nervous system in dorsal view. 1mm.
161) *Idem,* cerebral commissure cut. 1mm.
162) Charopidae sp., nervous system in dorsal view, cerebral commissure cut. 1mm.
163) Charopidae sp., nervous system in dorsal view. 1mm.
164) *Trachycystis capensis,* digestive tract. 2mm.
165) *Trachycystis capensis,* nervous system in dorsal view, cerebral commissure cut. 1.1mm.
166) *Trachycystis capensis,* nervous system in dorsal view. 1.1mm.

156



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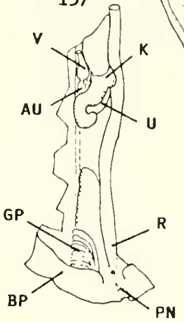

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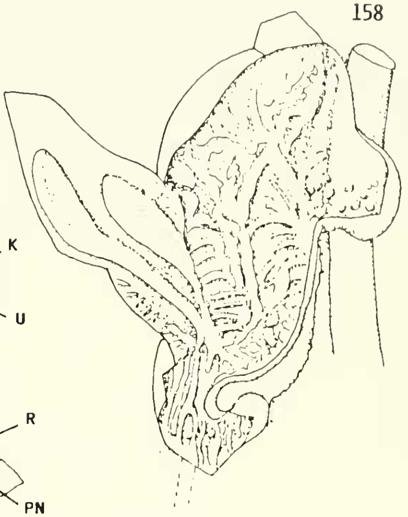

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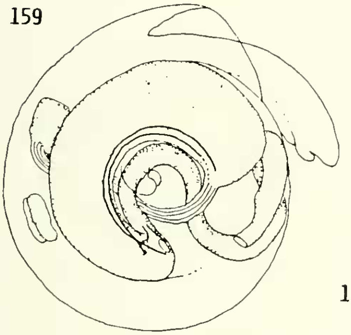

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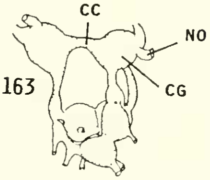

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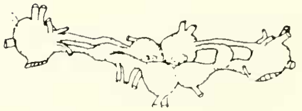

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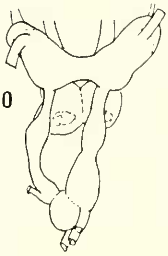

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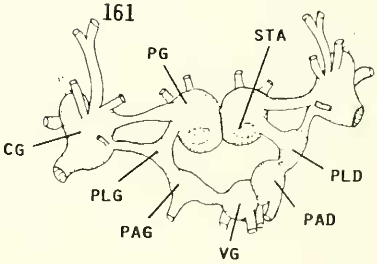

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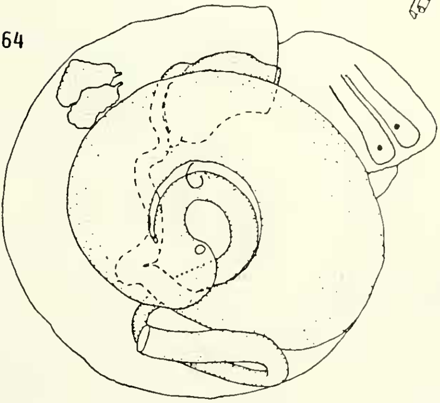

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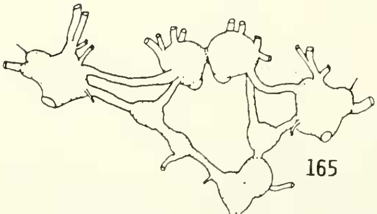

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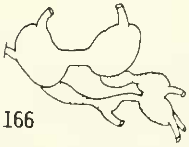
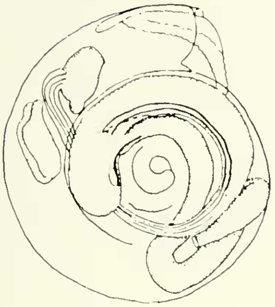


FIGS. 167–177: CHAROPIDAE, PUNCTIDAE
167) *Stephanoda binneyana*, digestive tract. 9mm.
168) *Stephanoda binneyana*, pulmonary complex. 9mm.
169) *Stephanoda binneyana*, kidney internal morphology. 4.5mm.
170) *Stephanoda binneyana*, nervous system in dorsal view. 2mm.
171) *Idem*, cerebral commissure cut. 2mm.
172) *Ranfurlya constanceae*, nervous system in dorsal view. 2mm.
173) *Idem*, cerebral commissure cut. 2mm.
174) *Ranfurlya constanceae*, digestive tract. 4mm.
175) *Cystopelta purpurea*, digestive tract. 0.8mm.
176) *Cystopelta purpurea*, nervous system in dorsal view. 2mm.
177) *Idem*, cerebral commissure cut. 2mm.

167



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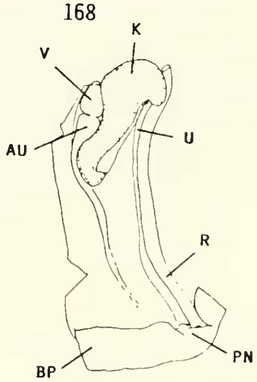

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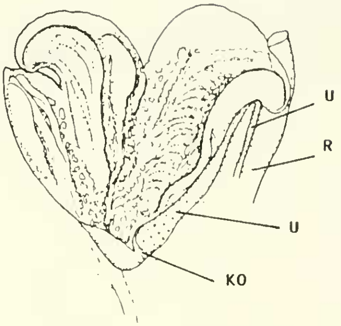

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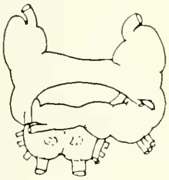

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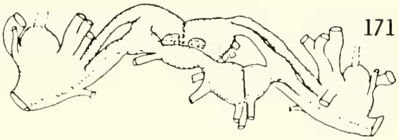

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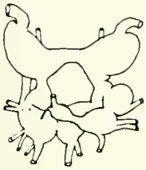

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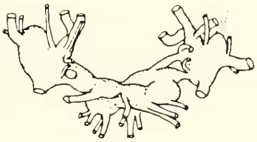

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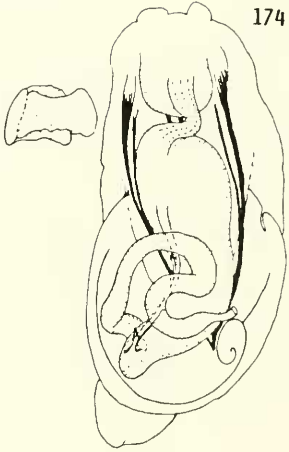

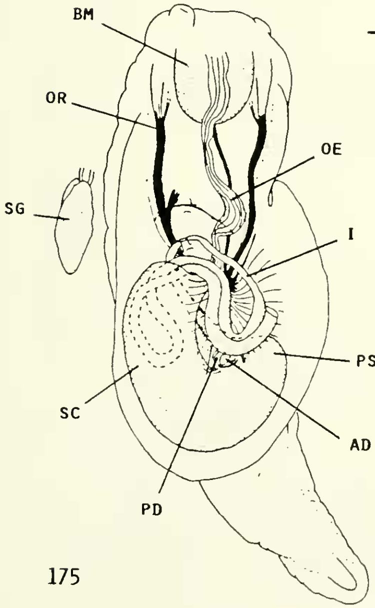

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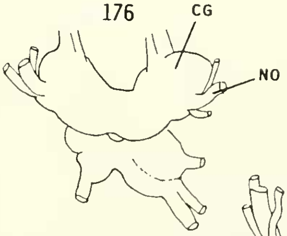

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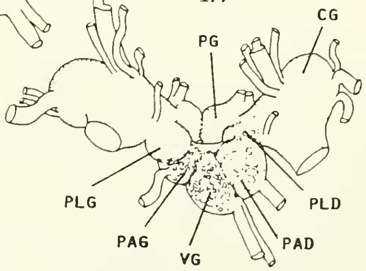
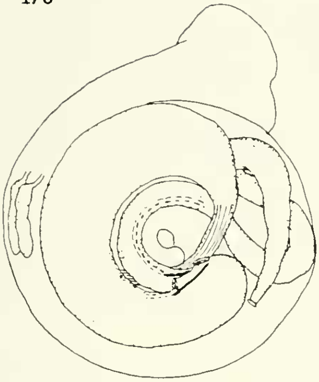


FIGS. 178–186: PUNCTIDAE, DISCIDAE
178) *Phrixgnathus erigone,* digestive tract. 2mm.
179) *Phrixgnathus erigone,* nervous system in dorsal view. 1mm.
180) *Idem,* cerebral commissure cut. 1mm.
181) *Paralaoma lateumbilicata,* digestive tract. 1mm.
182) *Phrixgnathus erigone,* internal morphology of cardiac arm of kidney. 4mm.
183) *Phrixgnathus erigone,* internal morphology of rectal arm of kidney. 4mm.
184) *Helicodiscus parallelus,* digestive tract. 1.3mm.
185) *Discus patulus,* pulmonary complex. 4.5mm.
186) *Discus patulus,* kidney internal morphology. 1mm.

178



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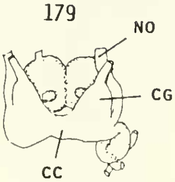

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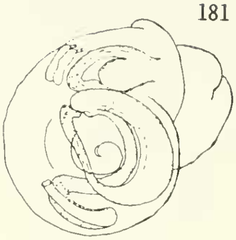

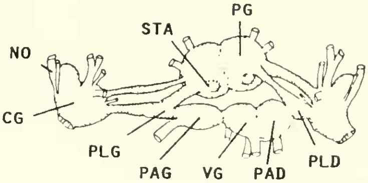

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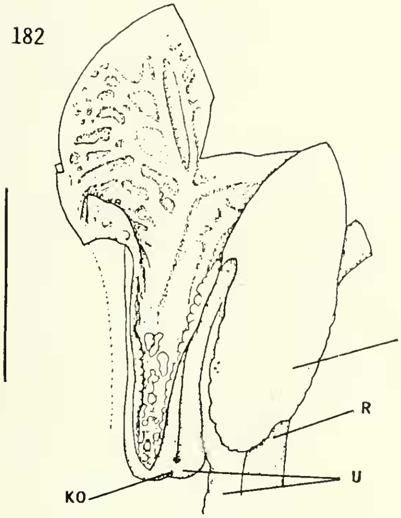

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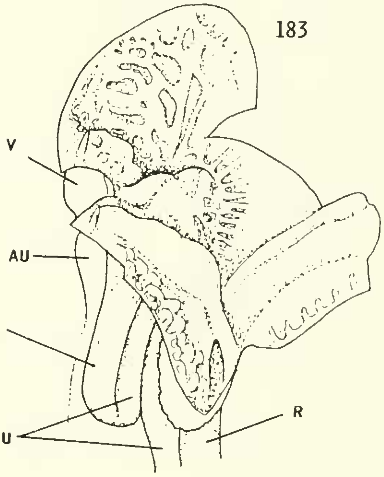

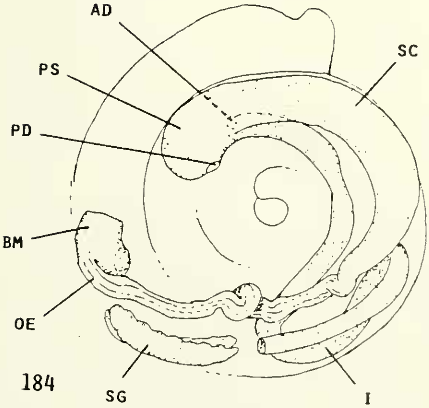

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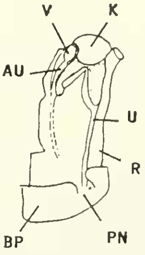

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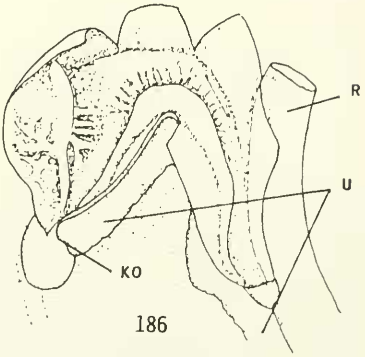
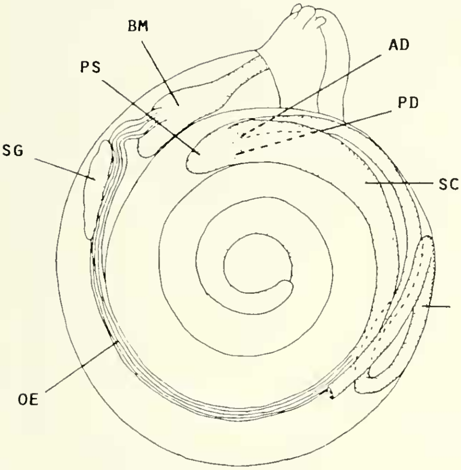


186

FIGS. 187–194: DISCIDAE
187) *Discus rotundatus*, digestive tract. 2.5mm.
188) *Discus rotundatus*, kidney internal morphology. 1mm.
189) *Discus rotundatus*, pulmonary complex. 4.5mm.
190) *Anguispira alternata*, digestive tract. 6mm.
191) *Anguispira alternata*, nervous system in dorsal view. 2mm.
192) *Idem*, cerebral commissure cut. 2mm.
193) *Anguispira alternata*, kidney internal morphology. 4.5mm.
194) *Anguispira alternata*. pulmonary complex. 9mm.

187



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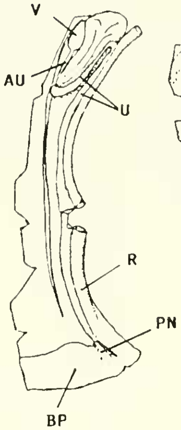

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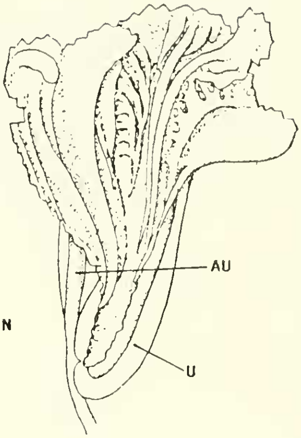

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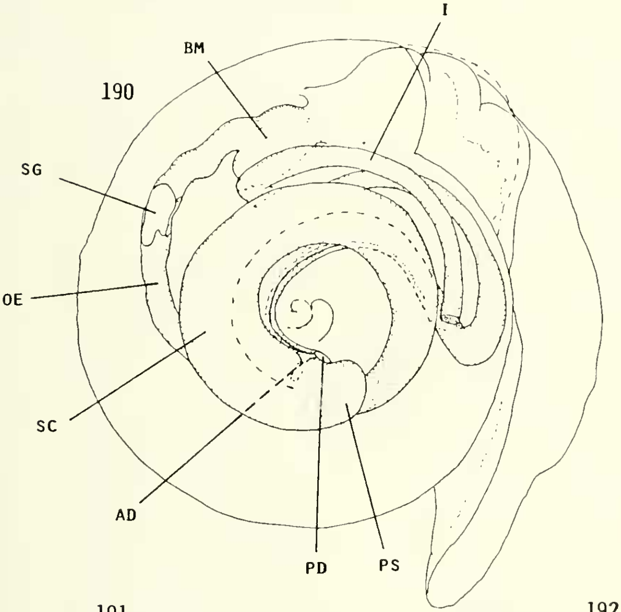

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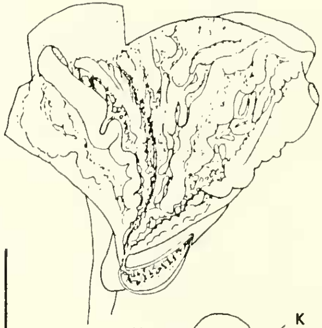

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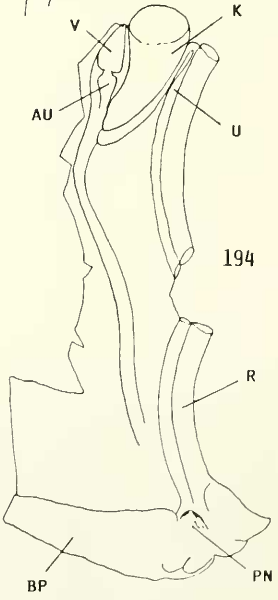

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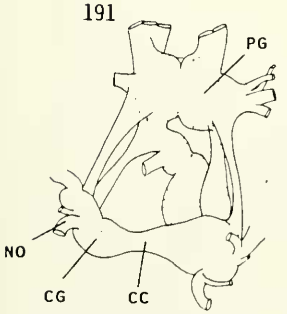

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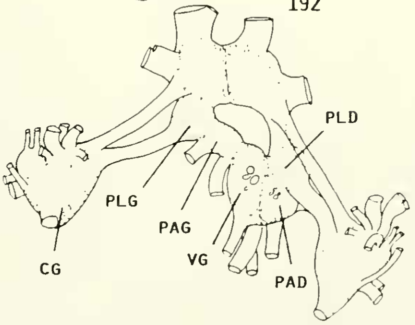
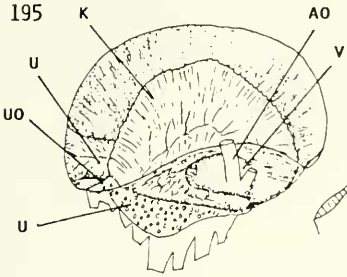


FIGS. 195–203: ARIONIDAE
195) *Hemphillia camelus,* pulmonary complex. 4mm.
196) *Idem,* pneumostome and secondary ureter opened. 4mm.
197) *Idem,* pericardium and primary ureter opened. 4mm.
198) *Idem,* detail: positions of kidney pore (KO) and reno-perocardial pore (PO). 4mm.
199) *Idem,* internal morphology of secondary ureter. 1.7mm.
200) *Hemphillia camelus,* digestive tract. 8mm.
201) *Hemphillia camelus,* morphology of gastric region. 4mm.
202) *Hemphillia camelus,* nervous system in dorsal view. 1.7mm.
203) *Idem,* cerebral commissure cut: internal side of left cerebral ganglion. 1.7mm.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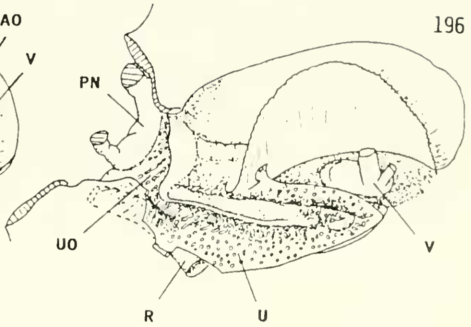
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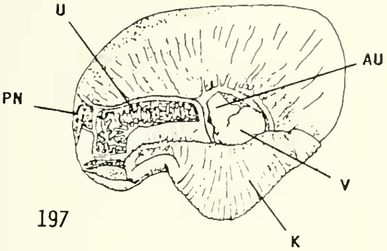
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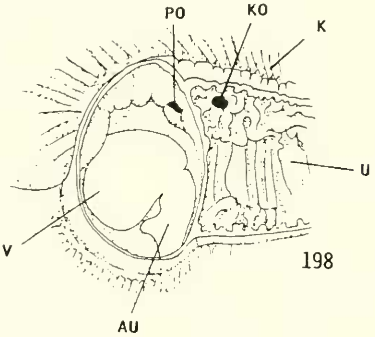
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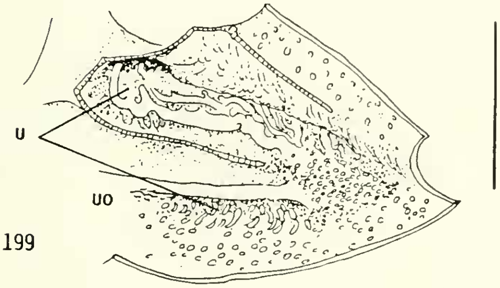
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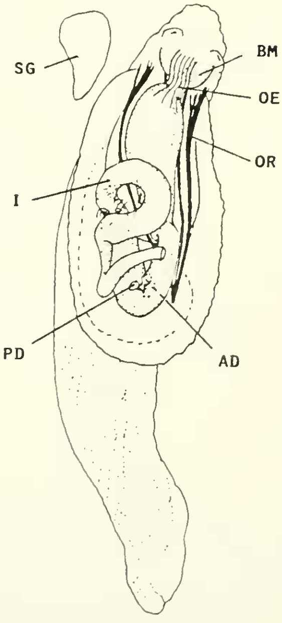
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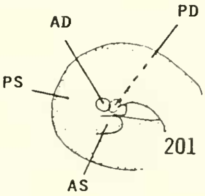
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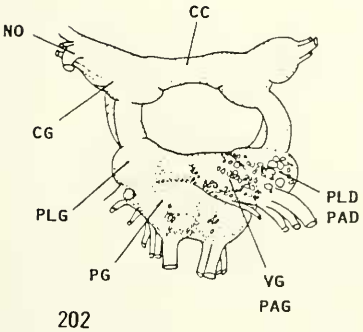
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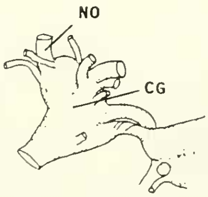
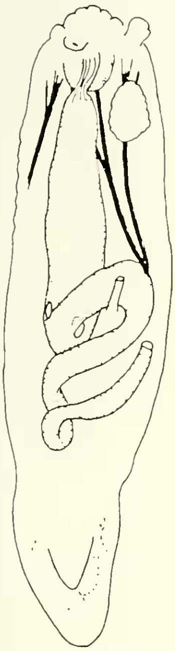

203

FIGS. 204–212: ARIONIDAE (including PHILOMYCINAE)
204) *Prophysaon humile*, digestive tract. 9mm.
205) *Arion rufus*, digestive tract. 13.8mm.
206) *Oopelta granulosa*, digestive tract. 13.8mm.
207) *Oopelta nigropunctata*, nervous system in dorsal view, cerebral commissure cut. 6mm.
208) *Oopelta nigropunctata*, nervous system in dorsal view. 6mm.
209) *Philomycus carolinianus*, ventral side of left cerebral ganglion. 2mm.
210) *Philomycus carolinianus*, nervous system in dorsal view. 2mm.
211) *Philomycus carolinianus*, pulmonary complex, secondary ureter opened, showing internal folds. 4mm.
212) *Philomycus carolinianus*, pulmonary complex, kidney cut and primary ureter opened. 4mm.

204



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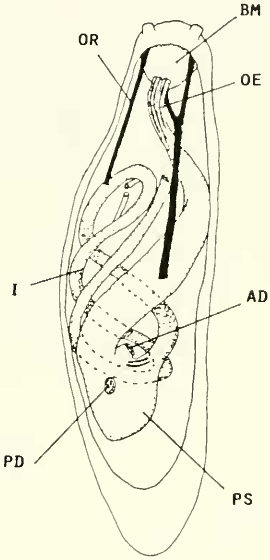

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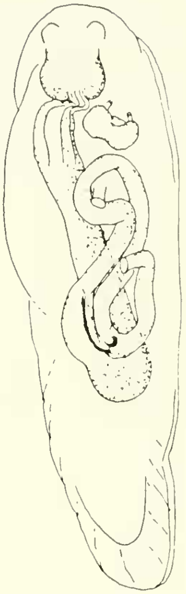

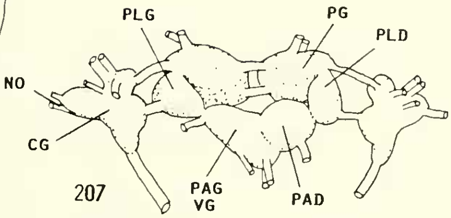

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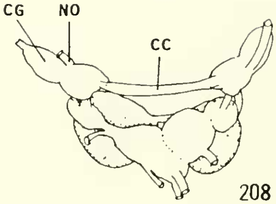

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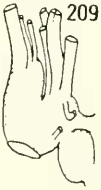

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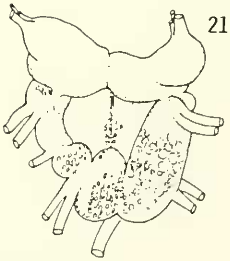

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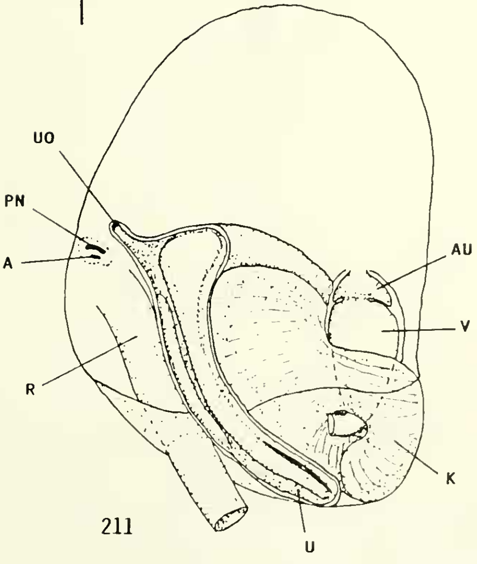

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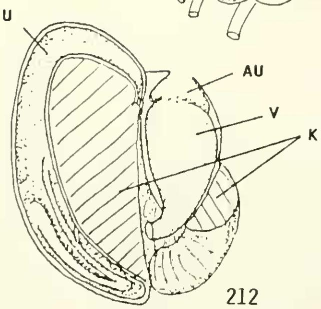
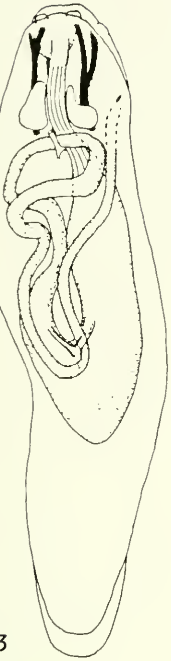


212

FIGS. 213–217: ARIONIDAE (including PHILOMYCINAE), PUNCTIDAE
213) *Philomycus bilineatus*, digestive tract. 8.6mm.
214) *Philomycus carolinianus*, diagram of relative positions of organs and of internal partitions in general cavity. 6mm.
215) *Philomycus carolinianus*, digestive tract. 6mm.
216) *Cystopelta purpurea*, diagram of relative positions of organs and of internal partitions in general cavity. 0.57mm.
217) *Hemphillia camelus*, diagram of relative positions of organs and of internal partitions in general cavity. 6mm.



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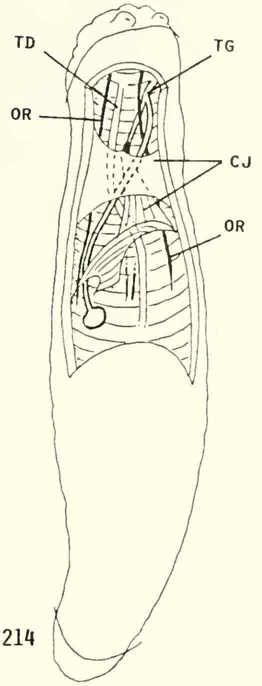

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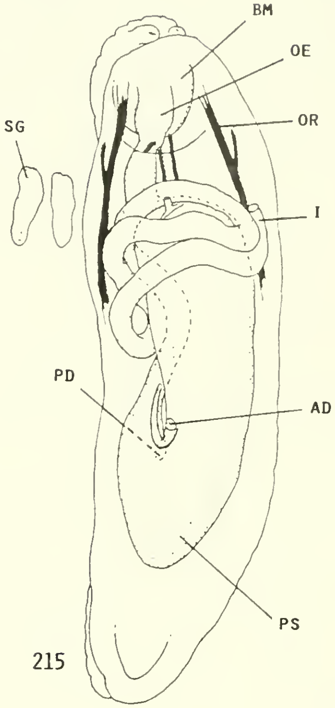

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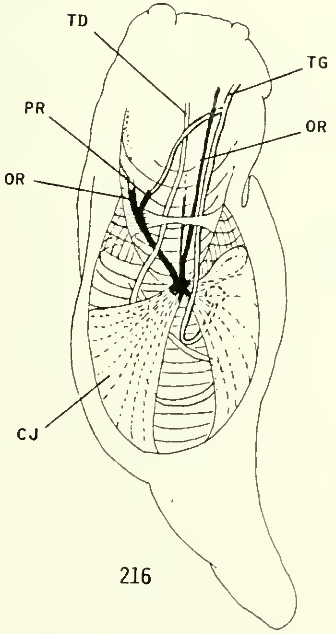

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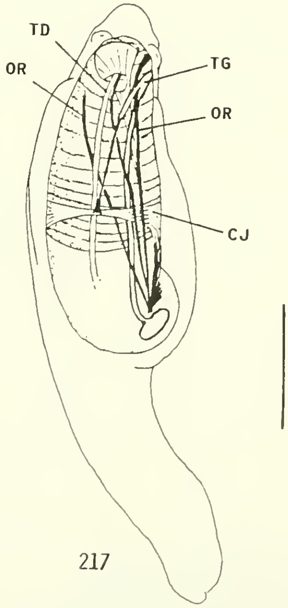
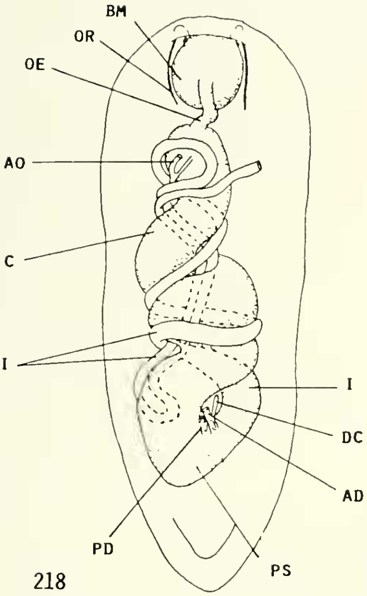


217

FIGS. 218–220: ATHORACOPHORIDAE
218) *Aneitea simrothi*, digestive tract. 7.6mm.
219) Athoracophoridae sp., digestive tract. 8mm.
220) Athoracophoridae sp., nervous system in dorsal view, cerebral commissure cut. 1mm.
(from Tillier, 1984a)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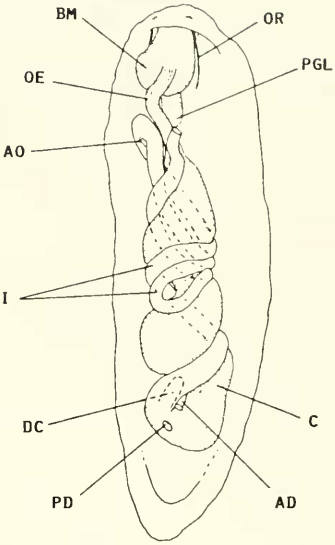
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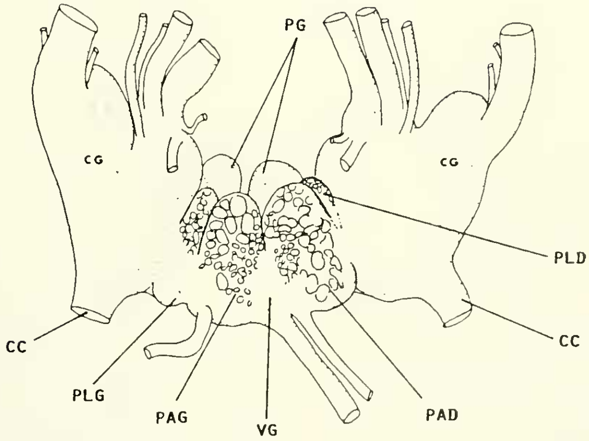
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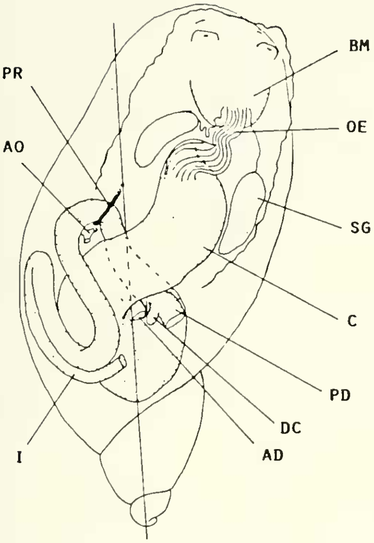
220

FIGS. 221–227: SUCCINEIDAE
221) *Succinea putris*, digestive tract. 6.4mm.
222) *Succinea putris*, nervous system in dorsal view. 2mm.
223) *Idem*, cerebral commissure cut. 2mm.
224) *Succinea putris*, pulmonary complex. 8mm.
225) *Succinea putris*, kidney internal morphology. 4.5mm.
226) *Succinea propinqua*, digestive tract. 4.5mm.
227) *Omalonyx matheroni*, digestive tract. 10mm.
(Figs. 221, 226, 227 from Tillier, 1984a)

221



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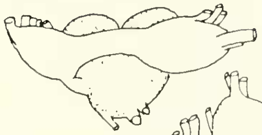

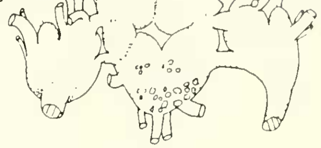

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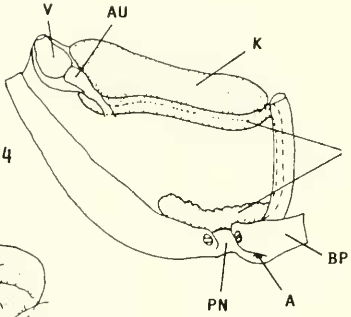

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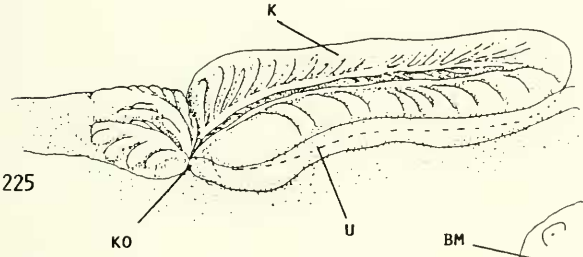

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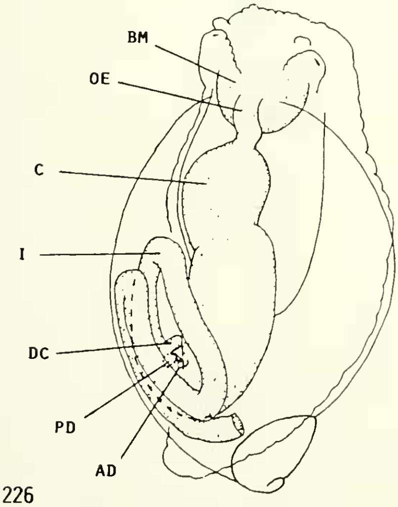

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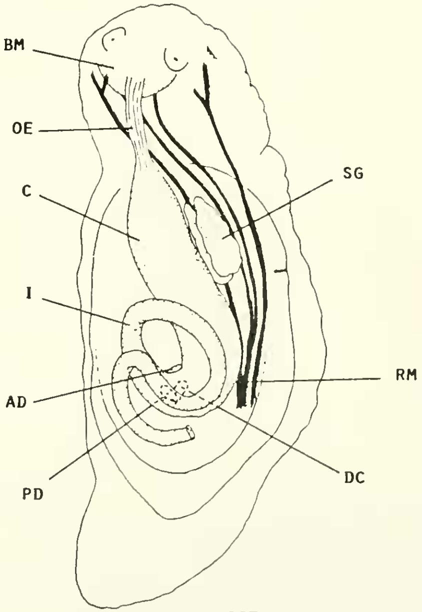
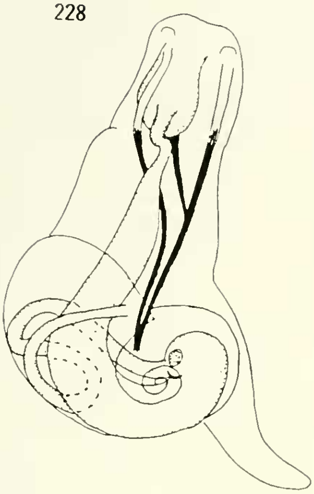


227

FIGS. 228–234: VITRINIDAE
228) *Phenacolimax major*, digestive tract. 3.8mm.
229) *Phenacolimax? ugandensis*, digestive tract. 5mm.
230) *Phenacolimax major*, nervous system in dorsal view. 2.2mm.
231) *Idem*, cerebral commissure cut. 2.2mm.
232) *Plutonia atlantica*, digestive tract. 7mm.
233) *Plutonia atlantica*, nervous system in dorsal view, cerebral commissure cut. 0.75mm.
234) *Plutonia atlantica*, nervous system in dorsal view. 0.75mm.

228



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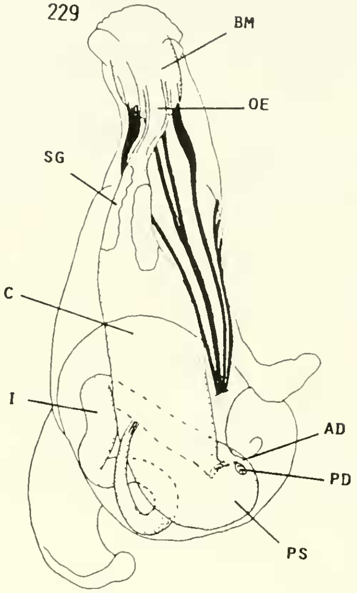

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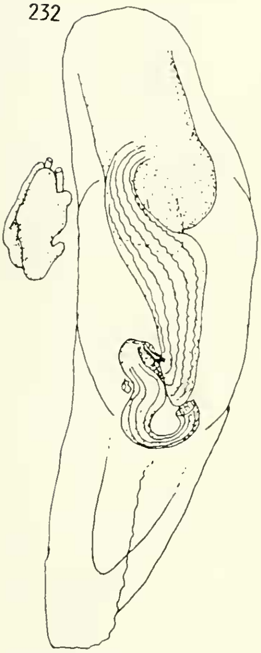

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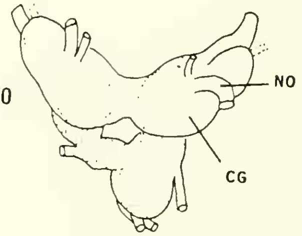

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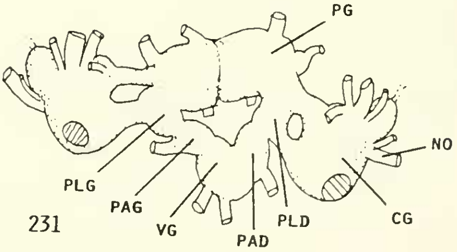

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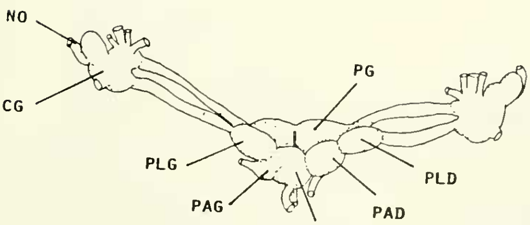

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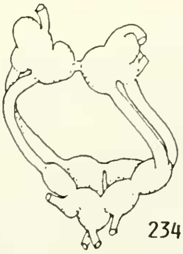
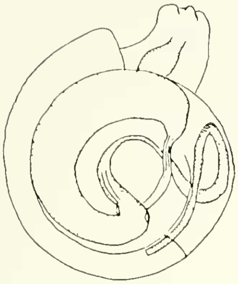


FIGS. 235–244: ZONITIDAE
235) *Vitrea crystallina,* digestive tract. 1.6mm.
236) *Vitrea crystallina,* kidney internal morphology. 1.4mm.
237) *Vitrea crystallina,* pulmonary complex. 1.6mm.
238) *Oxychilus draparnaudi,* nervous system in dorsal view. 2.25mm.
239) *Idem,* cerebral commissure cut. 2.25mm.
240) *Oxychilus draparnaudi,* digestive tract. 10.6mm.
241) *Aegopinella nitidula,* digestive tract. 4.3mm.
242) *Aegopinella nititula,* morphology of proximal intestine. 4.3mm.
243) *Aegopinella nitidula,* nervous system in dorsal view, cerebral commissure cut. 2mm.
244) *Aegopinella nitidula,* nervous system in dorsal view. 2mm.

235



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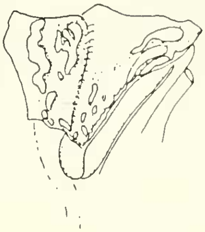

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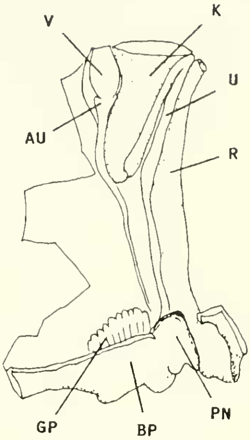

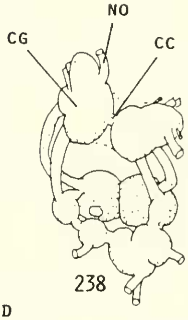

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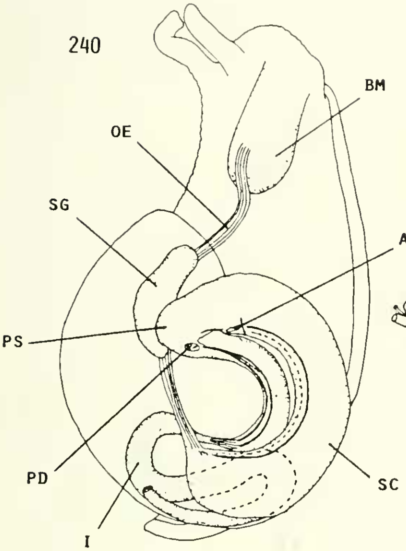

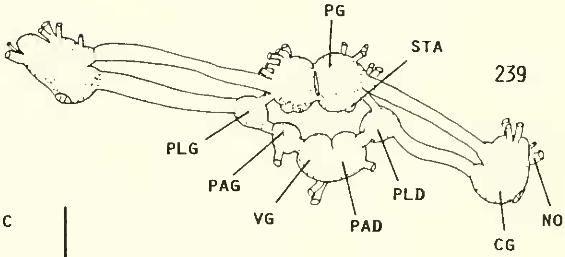

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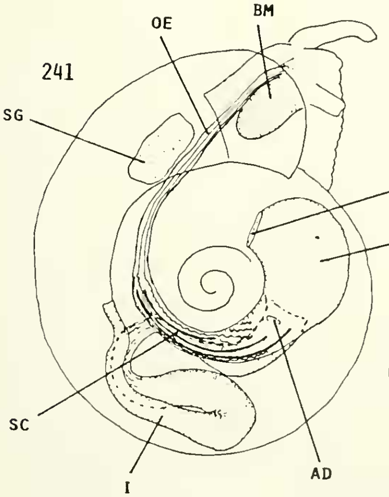

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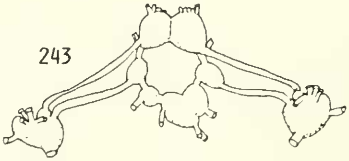

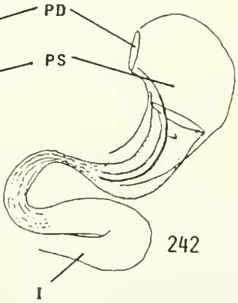

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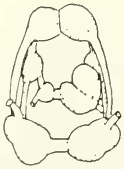
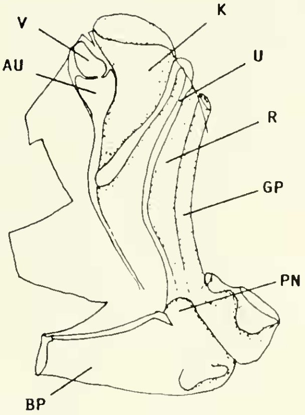


244

FIGS. 245–253: ZONITIDAE
245) *Aegopinella nitidula*, pulmonary complex. 4.7mm.
246) *Aegopinella nitidula*, kidney internal morphology. 3.3mm.
247) *Daudebardia lederi*, digestive tract. 4.3mm.
248) *Mesomphix inornatus*, digestive tract. 5mm.
249) *Mesomphix inornatus*, pulmonary complex. 7mm.
250) *Daudebardia* sp., nervous system in dorsal view, cerebral commissure cut. 3.3mm.
251) *Daudebardia* sp., nervous system in dorsal view. 3.3mm.
252) *Mesomphix inornatus*, nervous system in dorsal view. 2mm.
253) *Idem*, cerebral commissure cut. 2mm.

245



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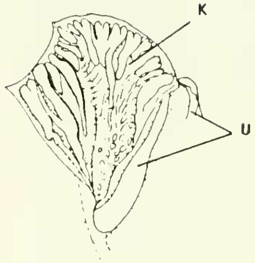

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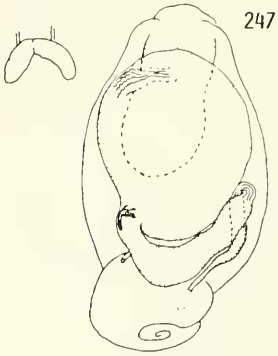

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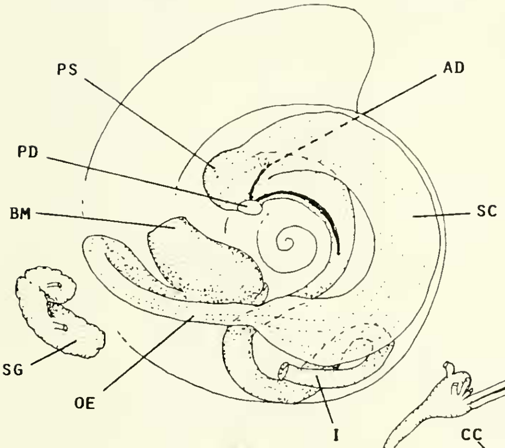

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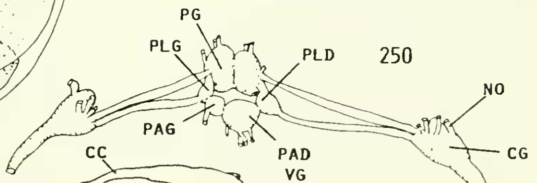

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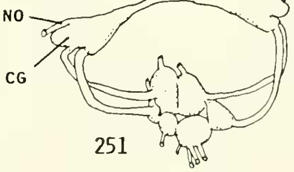

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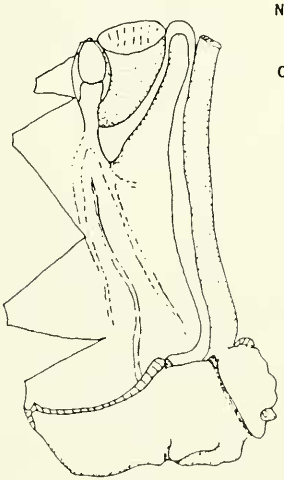

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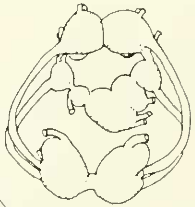

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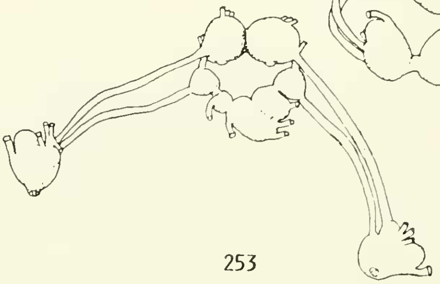
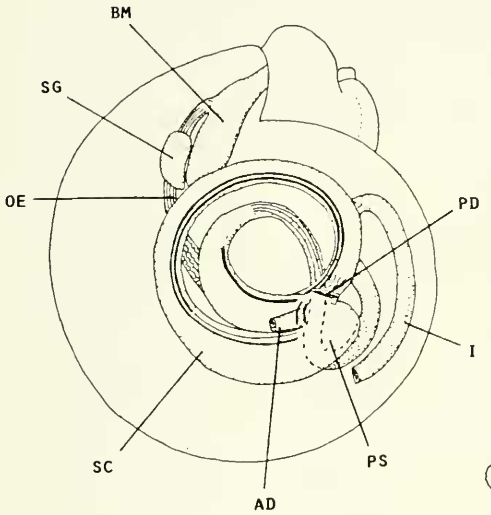


FIGS. 254–258: ZONITIDAE
254) *Zonites algirus,* digestive tract. 16mm.
255) *Zonites algirus,* pulmonary complex. 11.6mm.
256) *Zonites algirus,* kidney internal morphology. 6.6mm.
257) *Zonites algirus,* nervous system in dorsal view. 6mm.
258) *Idem,* cerebral commissure cut. 6mm.

254



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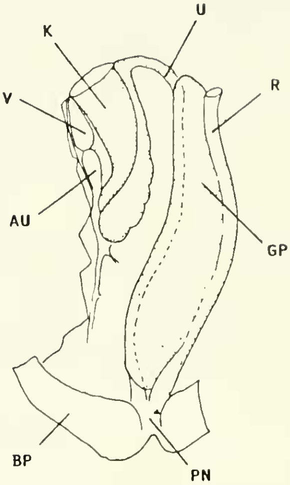

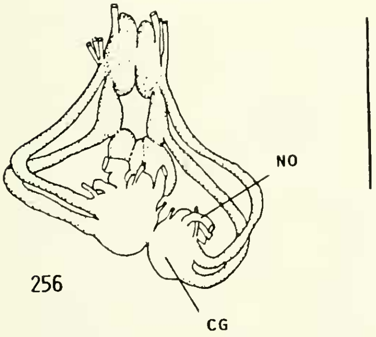

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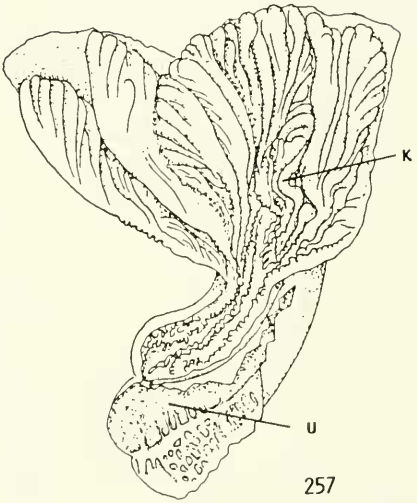

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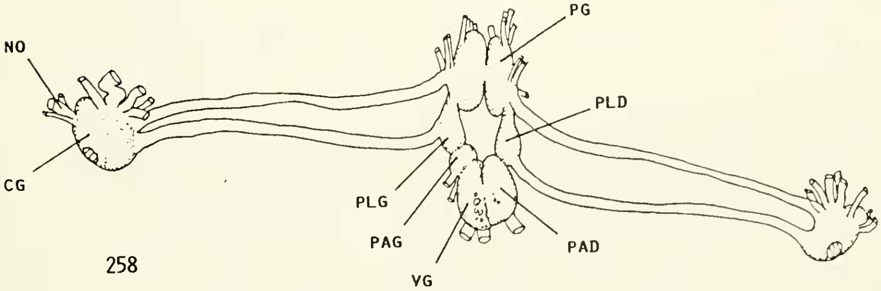

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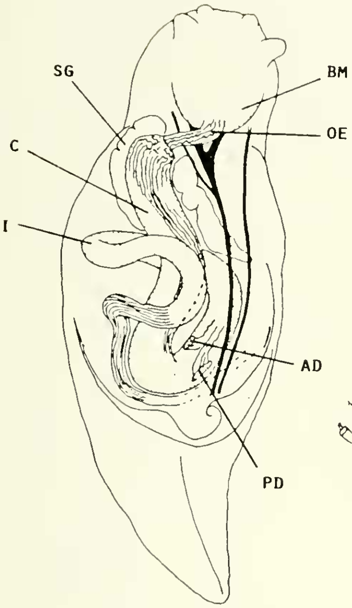
FIGS. 259–268: PARMACELLIDAE, LIMACIDAE, MILACIDAE
259) *Parmacella valenciennesi,* digestive tract. 11mm.
260) *Parmacella deshayesi,* nervous system in dorsal view, cerebral commissure cut. 3.15mm.
261) *Parmacella valenciennesi,* nervous system in dorsal view, cerebral commissure cut. 3.15mm.
262) *Parmacella valenciennesi,* nervous system in dorsal view. 3.15mm.
263) *Limax maximus,* digestive tract. 20.6mm.
264) *Milax gagates,* digestive tract. 12.7mm.
265) *Limax maximus,* nervous system in dorsal view. 3mm.
266) *Idem,* cerebral commissure cut. 3mm.
267) *Milax gagates,* nervous system in dorsal view. 2.5mm.
268) *Idem,* cerebral commissure cut. 2.5mm.

259



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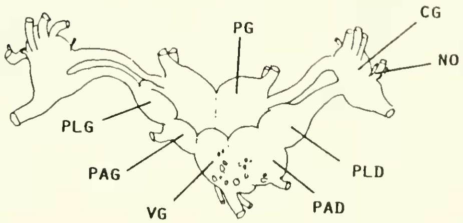

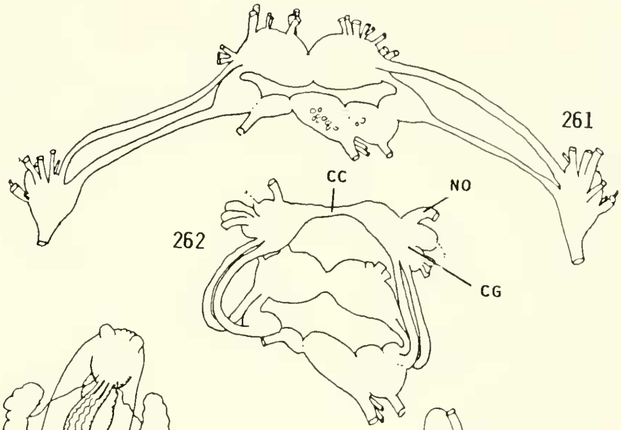

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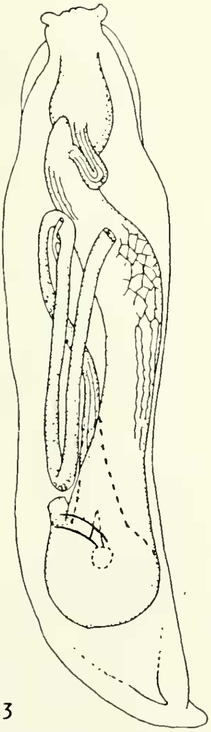

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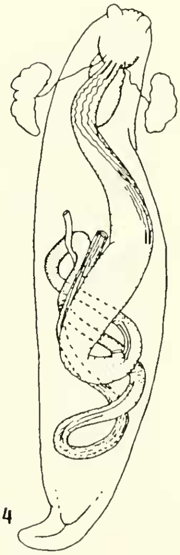

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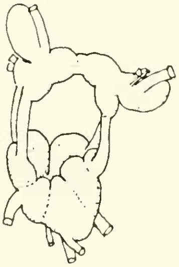

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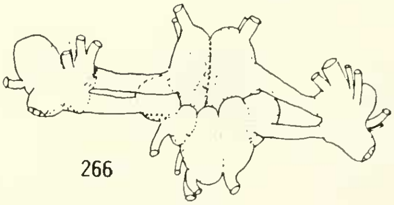

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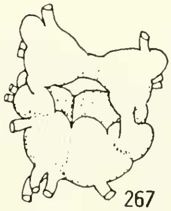

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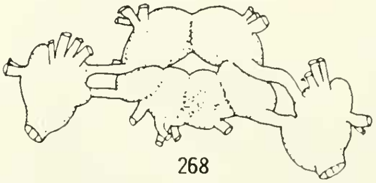

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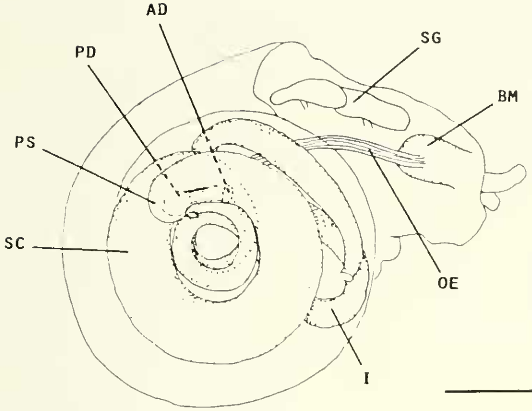
FIGS. 269–277: ZONITIDAE (GASTRODONTINAE)
269) *Ventridens acera,* digestive tract. 9mm.
270) *Ventridens acera,* nervous system in dorsal view. 4.5mm.
271) *Idem,* cerebral commissure cut. 4.5mm.
272) *Gastrodonta interna,* nervous system in dorsal view. 1mm.
273) *Idem,* cerebral commissure cut. 1mm.
274) *Ventridens acera,* pulmonary complex. 13.8mm.
275) *Ventridens acera,* kidney internal morphology. 2mm.
276) *Gastrodonta interna,* digestive tract. 4.5mm.
277) *Zonitoides arboreus,* digestive tract. 2mm.

269



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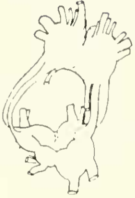

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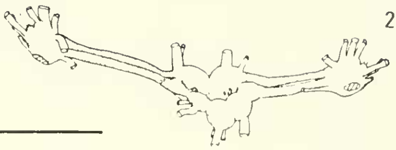

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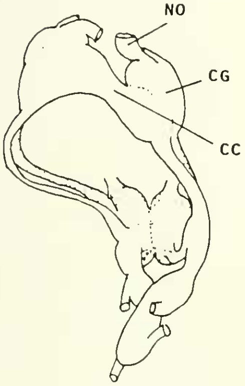

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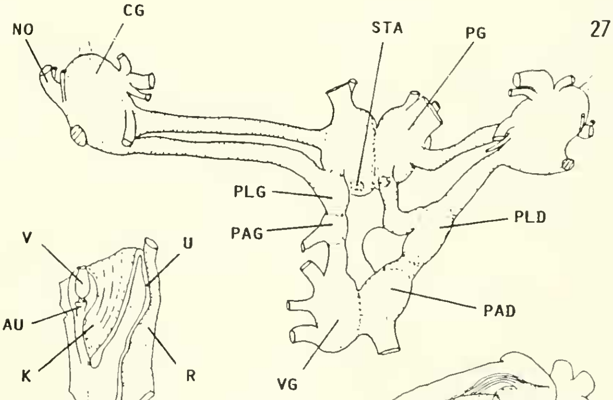

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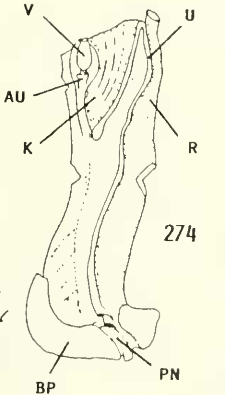

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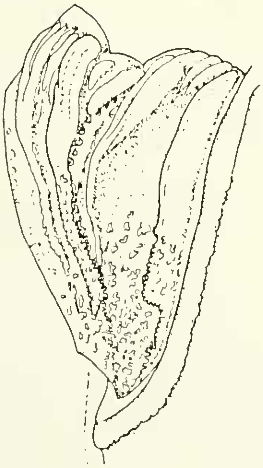

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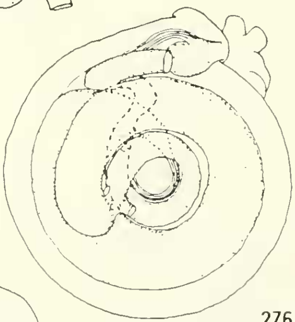

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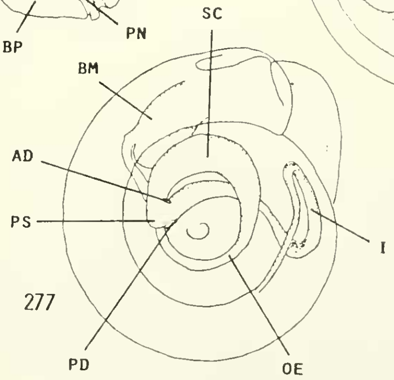
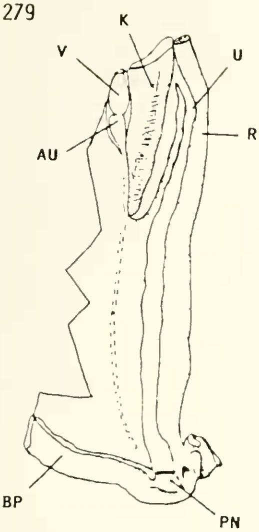


FIGS. 278–287: TROCHOMORPHIDAE, EUCONULIDAE
278) *Trochomorpha* sp., digestive tract. 3.8mm.
279) *Trochomorpha* sp., pulmonary complex. 8.5mm.
280) *Conibycus* cf. *dahli*, digestive tract. 4mm.
281) *Trochomorpha* sp., nervous system in dorsal view. 2mm.
282) *Idem*, cerebral commissure cut. 2mm.
283) *Discoconulus* sp. 1, nervous system in dorsal view. 1.4mm.
284) *Idem*, cerebral commissure cut. 1.4mm.
285) *Discoconulus* sp.1, pulmonary complex. 2.7mm.
286) *Discoconulus* sp.1, digestive tract. 4.7mm.
287) *Discoconulus* sp.2, pulmonary complex. 2.7mm.

279



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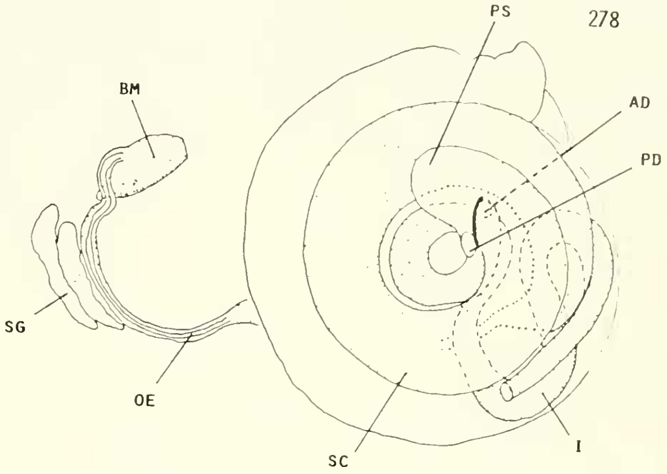

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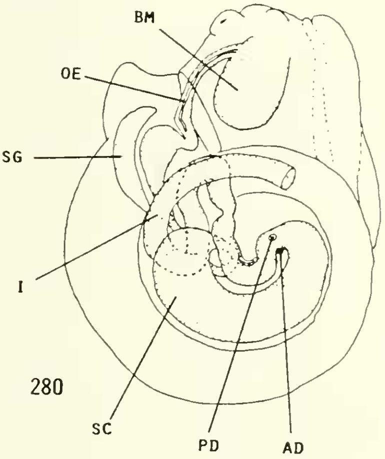

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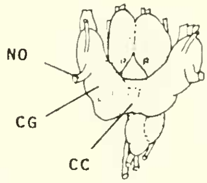

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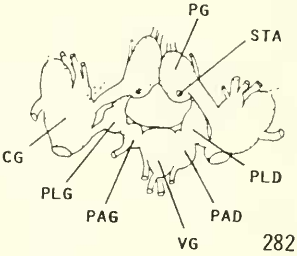

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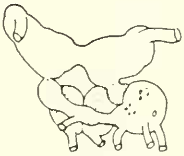

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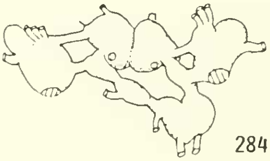

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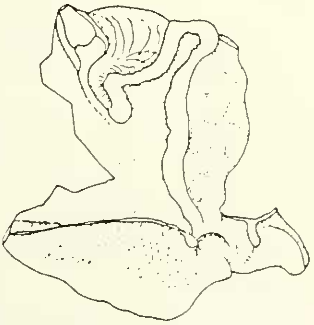

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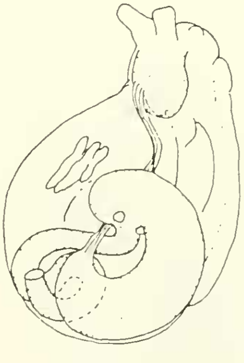

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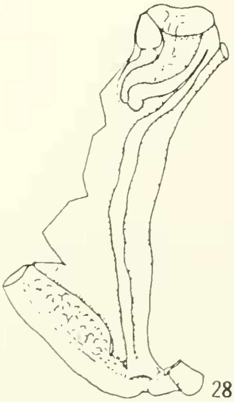
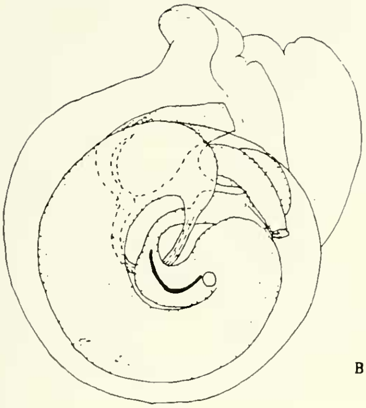


FIGS. 288–295: EUCONULIDAE
288) *Coneuplecta* sp.3, digestive tract. 2.5mm.
289) *Coneuplecta* sp.3, pulmonary complex. 3.7mm.
290) *Coneuplecta* sp.3, nervous system in dorsal view. 1.3mm.
291) *Idem,* cerebral commissure cut. 1.3mm.
292) *Coneuplecta* sp.1, digestive tract. 3mm.
293) *Coneuplecta* sp.2, pulmonary complex. 3.7mm.
294) *Vitrinopsis* sp.1, pulmonary complex. 2.5mm.
295) *Vitrinopsis* sp.1, digestive tract. 3mm.

288



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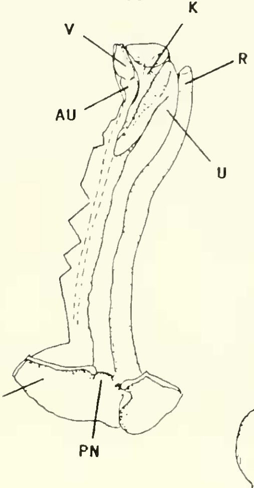

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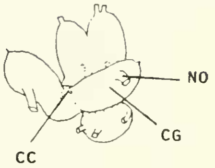

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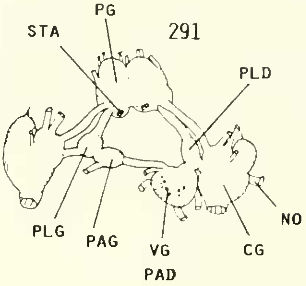

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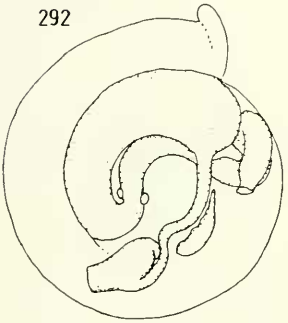

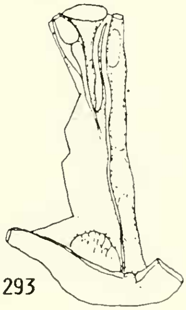

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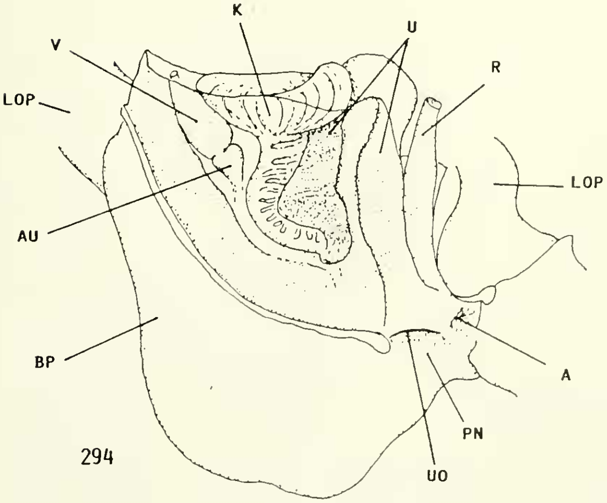

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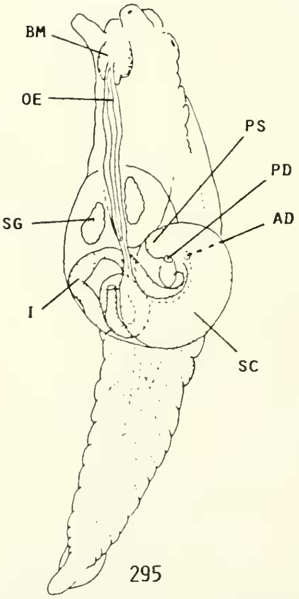

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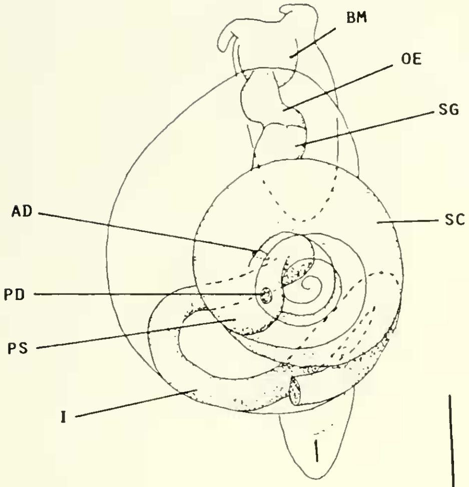
FIGS. 296–302: HELICARIONIDAE (HELICARIONINAE)
296) *Kalidos oleatus,* digestive tract. 19.5mm.
297) *Kalidos oleatus,* pulmonary complex. 19.5mm.
298) Helicarioninae sp., digestive tract. 4.8mm.
299) Helicarioninae sp., nervous system in dorsal view. 3.9mm.
300) Idem, cerebral commissure cut. 3.9mm.
301) Helicarioninae sp., pulmonary complex. 4.8mm.
302) Helicarioninae sp., kidney internal morphology. 2.3mm.
(Figs. 296, 298 from Tillier, 1984a)

296



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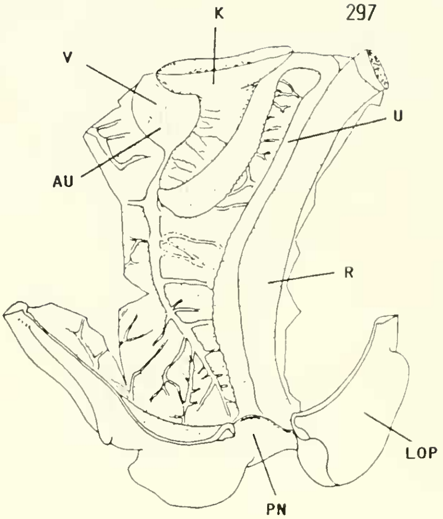

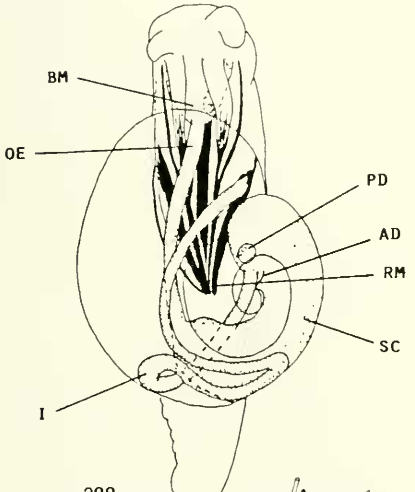

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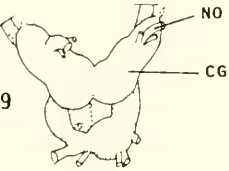

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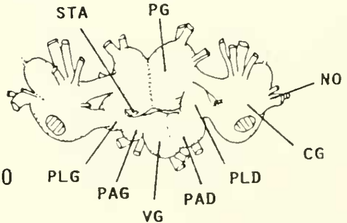

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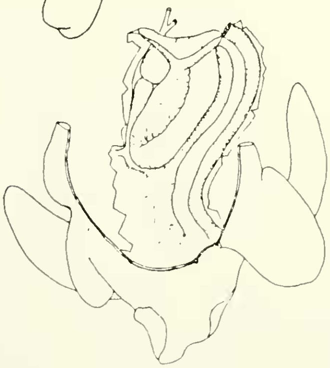

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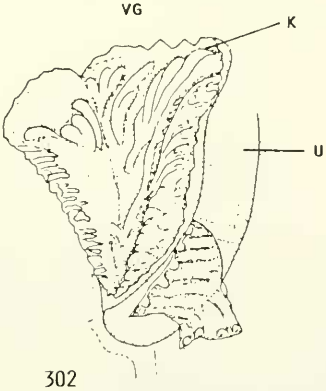
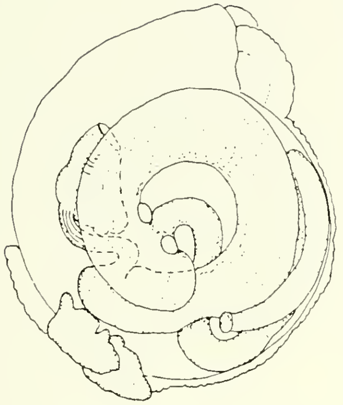


302

FIGS. 303–309: HELICARIONIDAE (DYAKIINAE, PARMARIONINAE)
303) *Everettia corrugata*, digestive tract. 9.2mm.
304) *Everettia corrugata*, pulmonary complex. 9.2mm.
305) *Everettia corrugata*, nervous system in dorsal view. 2.5mm.
306) *Idem*, cerebral commissure cut. 2.5mm.
307) *Parmarion martensi*, digestive tract. 3.1mm.
308) *Microparmarion pollonerai*, nervous system in dorsal view. 2.6mm.
309) *Idem*, cerebral commissure cut. 2.6mm.
(Fig. 307 from Tillier, 1984a)

303



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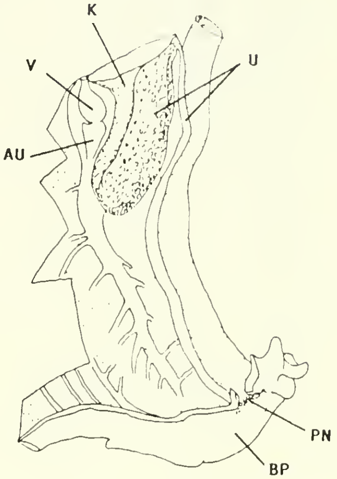

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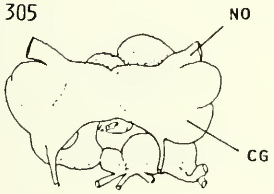

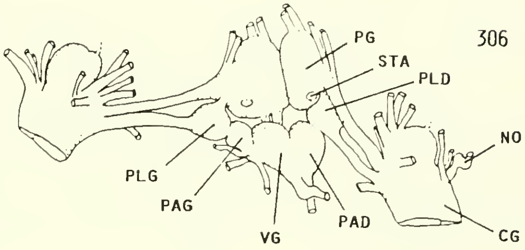

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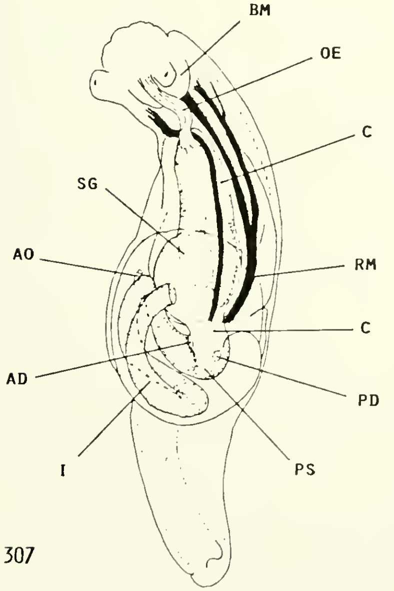

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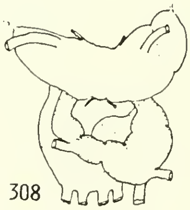

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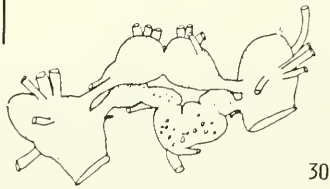
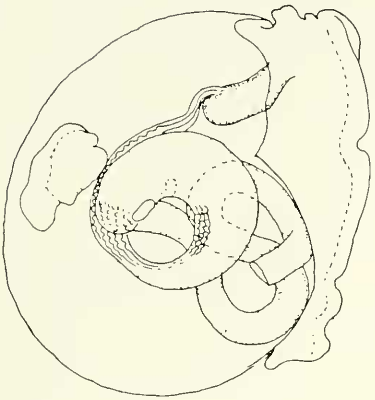


309

FIG. 310–317: HELICARIONIDAE (ARIOPHANTINAE, TROCHOZONITINAE)
310) *Hemiplecta humphreysiana*, digestive tract. 2cm.
311) *Mariaella dussumieri*, digestive tract. 10.6mm.
312) *Hemiplecta humphreysiana*, nervous system in dorsal view. 5.1mm.
313) *Idem*, cerebral commissure cut. 5.1mm.
314) *Trochozonites percarinatus*, nervous system in dorsal view. 2mm.
315) *Idem*, cerebral commissure cut. 2mm.
316) *Trochozonites percarinatus*, digestive tract. 5.2mm.
317) *Trochozonites percarinatus*, pulmonary complex. 8mm.

310



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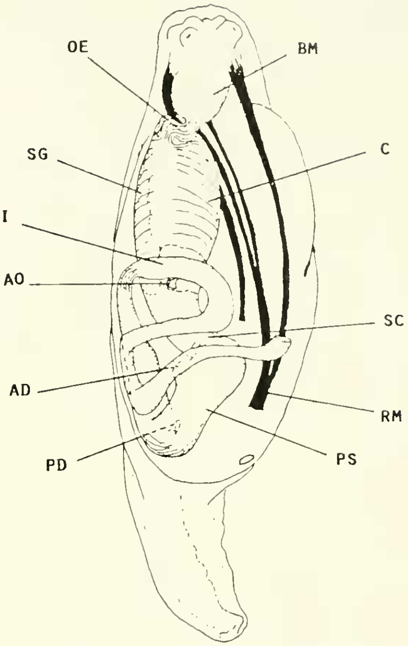

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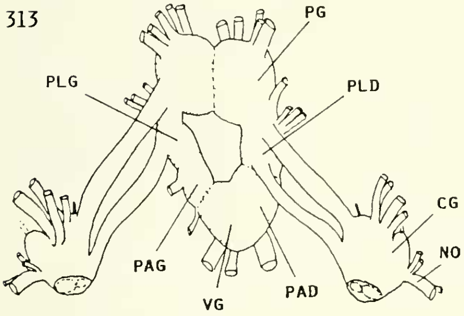

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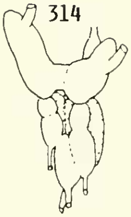

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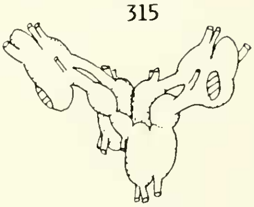

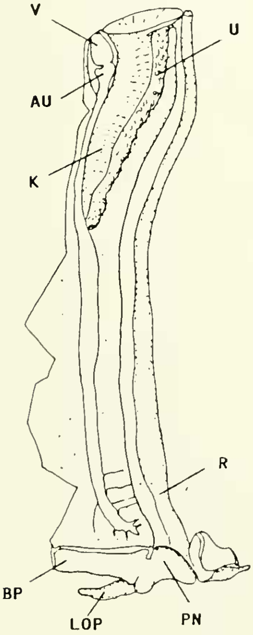

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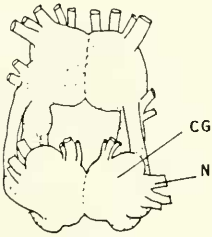

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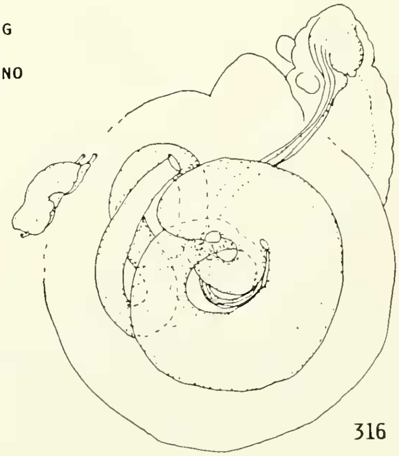
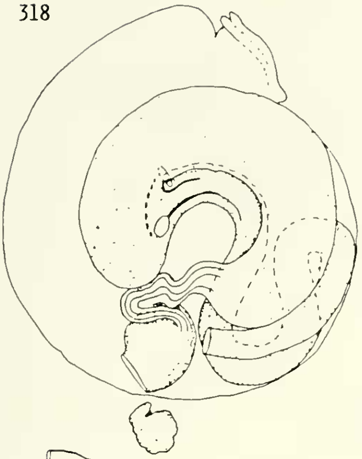


316

FIGS. 318–324: HELICARIONIDAE (UROCYCLINAE, GYMNARIONINAE)
318) *Trochonanina simulans*, digestive tract. 6.2mm.
319) *Trochonanina simulans*, nervous system in dorsal view. 2.25mm.
320) *Idem*, cerebral commissure cut. 2.25mm.
321) *Acantharion browni*, nervous system in dorsal view. 3.1mm.
322) *Idem*, cerebral commissure cut. 3.1mm.
323) *Acantharion browni*, digestive tract. 10mm.
324) *Gymnarion sowerbyanus*, digestive tract. 10mm.
(Figs. 321–324 from Binder & Tillier, 1986)

318



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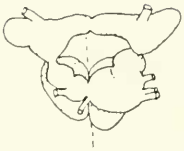

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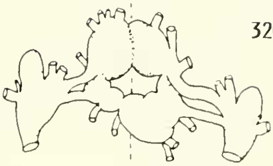

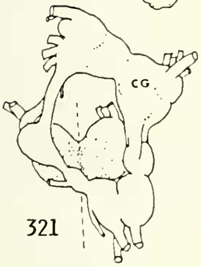

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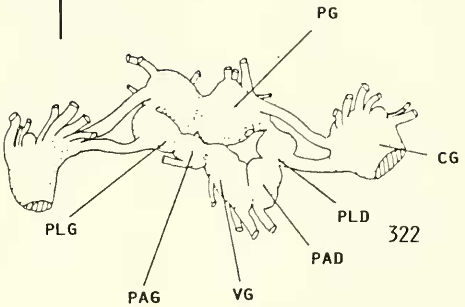

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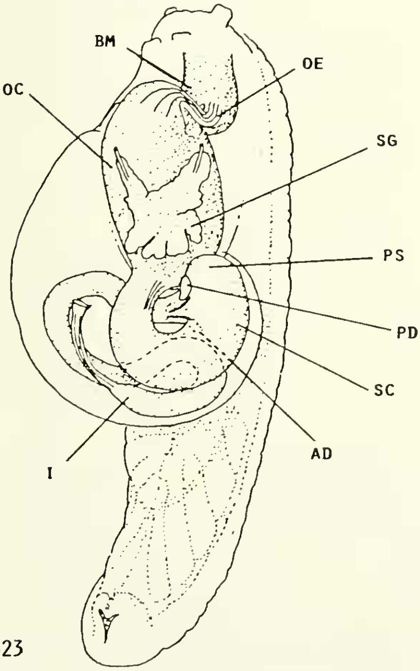

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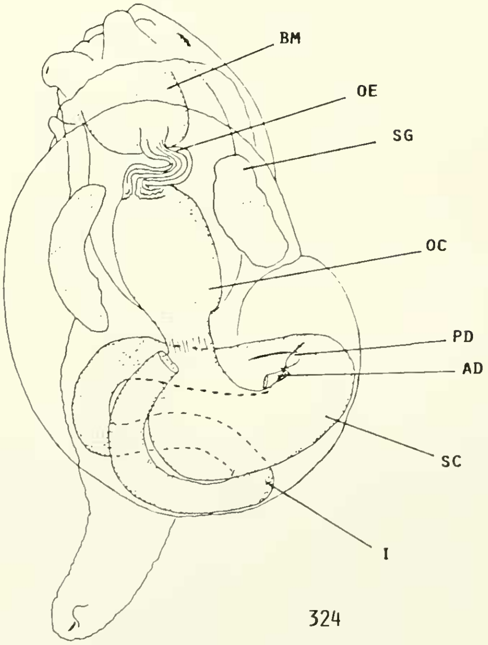
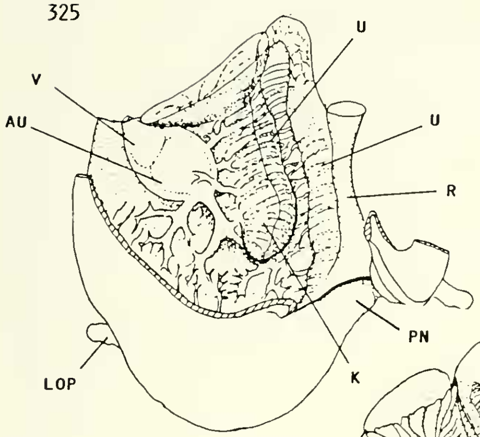


324

FIGS. 325–333: HELICARIONIDAE (GYMNARIONINAE, UROCYCLINAE)
325) *Acantharion browni*, pulmonary complex. 5.6mm.
326) *Gymnarion sowerbyanus*, pulmonary complex. 8.5mm.
327) *Acantharion browni*, kidney internal morphology. 5.6mm.
328) *Granularion lamottei*, digestive tract. 7.6mm.
329) *Mesafricarion maculifer*, digestive tract. 6mm.
330) *Granularion lamottei*, cerebral ganglia in a dorsal view. 3.8mm.
331) *Idem.*, nervous system in dorsal view, cerebral commissure cut. 3.8mm.
332) *Mesafricarion maculifer*, nervous system in dorsal view. 2.5mm.
333) *Idem*, cerebral commissure cut. 2.5mm.
(Figs. 328, 329 from Tillier, 1984a)



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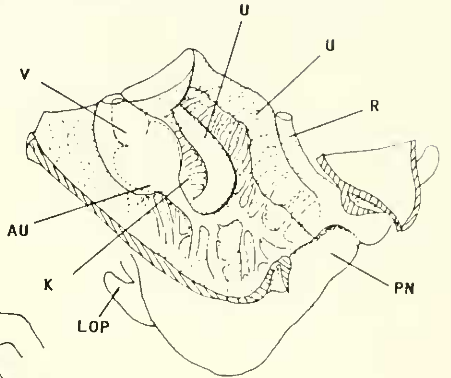

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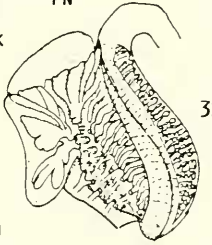

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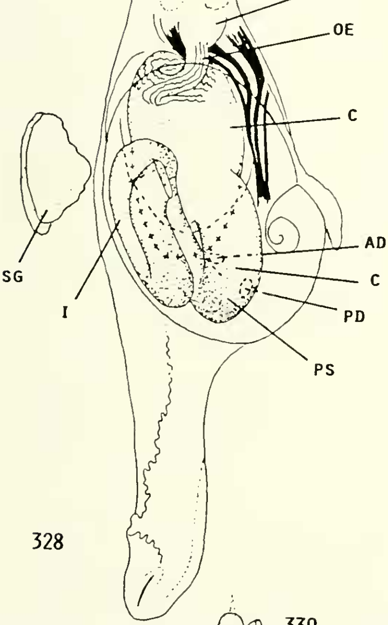

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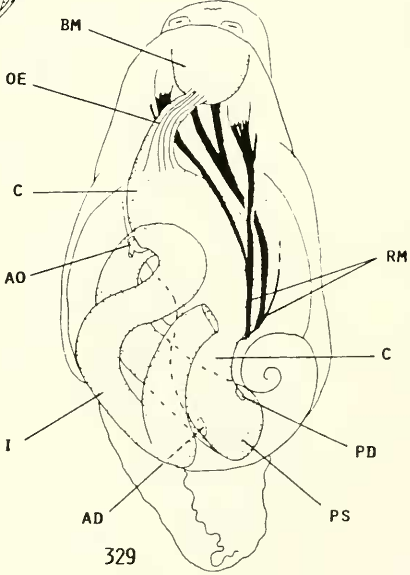

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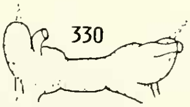

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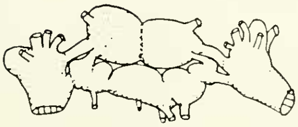

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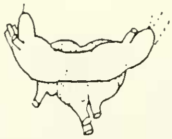

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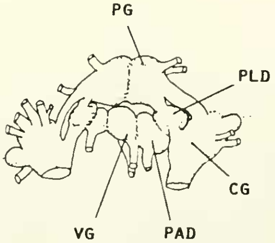
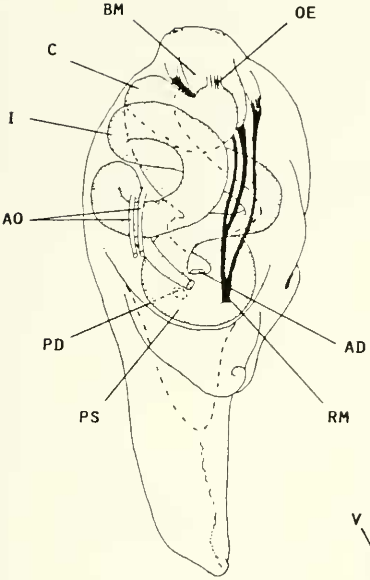


333

FIGS. 334–340: HELICARIONIDAE (UROCYCLINAE)
334) *Tresia parva,* digestive tract. 2.5mm.
335) *Estria?* sp., digestive tract. 5mm.
336) *Atoxon pallens,* kidney internal morphology. 2.5mm.
337) *Elisolimax madagascariensis,* digestive tract. 5mm.
338) *Atoxon pallens,* digestive tract. 5mm.
339) *Atoxon pallens,* nervous system in dorsal view. 1mm.
340) *Idem,* cerebral commissure cut. 1mm.
(Figs. 334, 335, 337, 338 from Tillier, 1984a)

334



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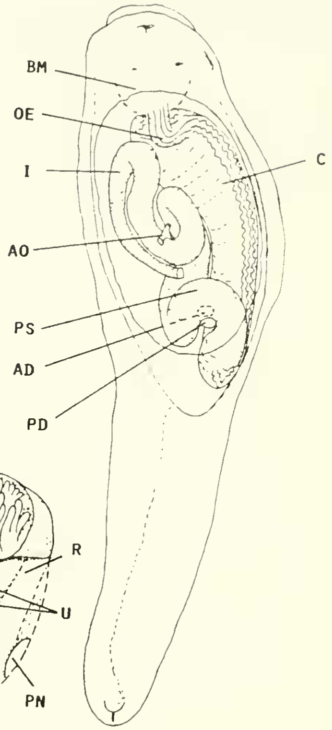

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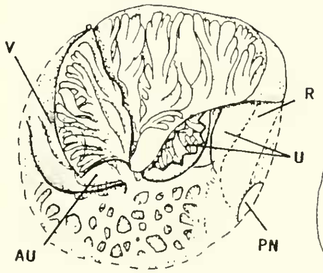

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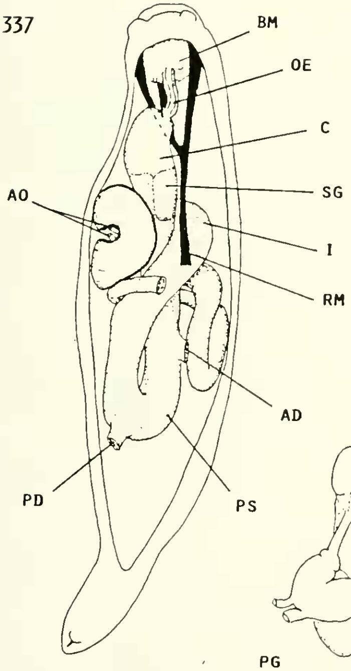

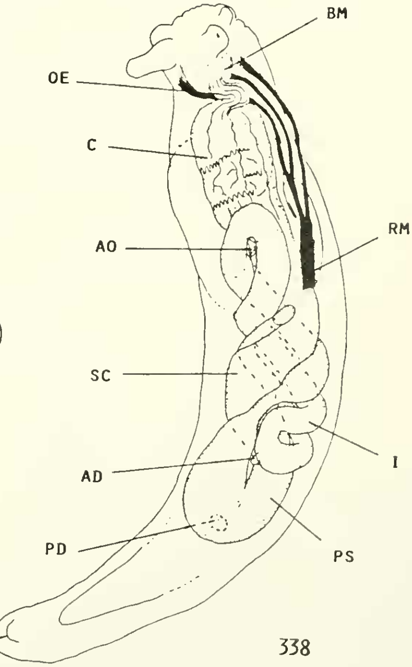

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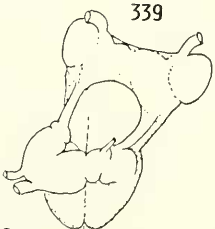
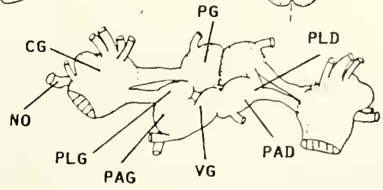
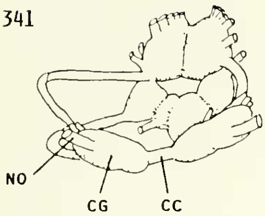




340

FIGS. 341–348: SUBULINIDAE
341) *Bocageia carpenteri*, nervous system in dorsal view. 2.5mm.
342) *Idem*, cerebral commissure cut. 2.5mm.
343) *Bocageia carpenteri*, digestive tract. 11.3mm.
344) *Pseudoglessula hessei*, digestive tract. 4.5mm.
345) *Pseudoglessula hessei*, nervous system in dorsal view. 2mm.
346) *Idem*, cerebral commissure cut. 2mm.
347) *Pseudoglessula hessei*, pulmonary complex. 5mm.
348) *Pseudoglessula hessei*, kidney internal morphology. 2.8mm.

341



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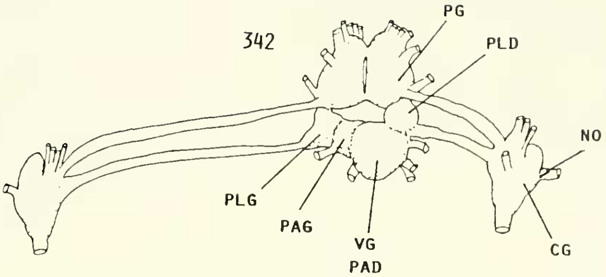

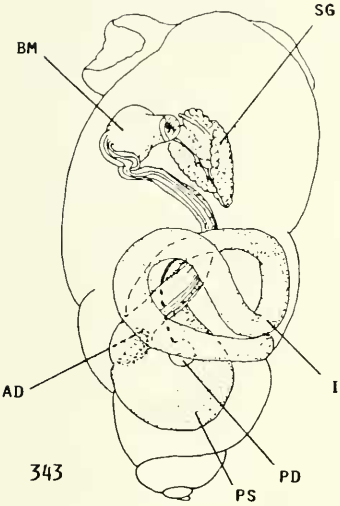

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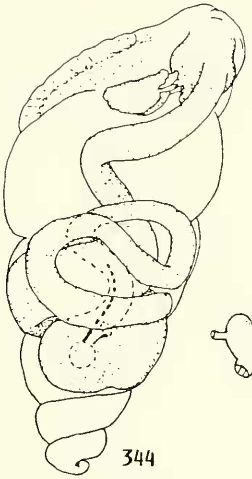

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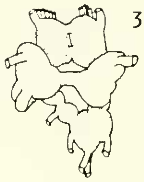

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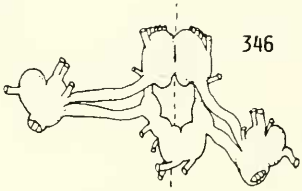

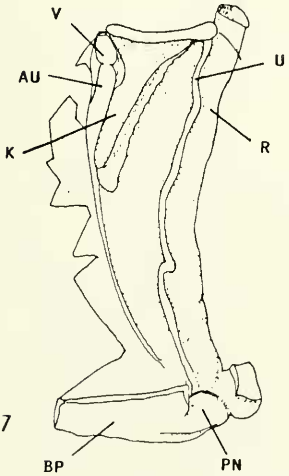

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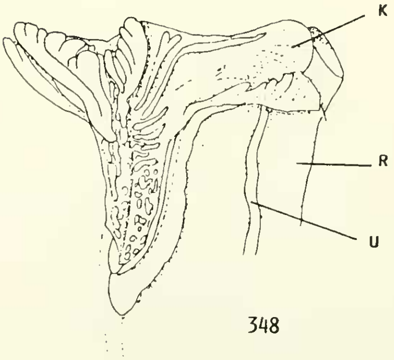
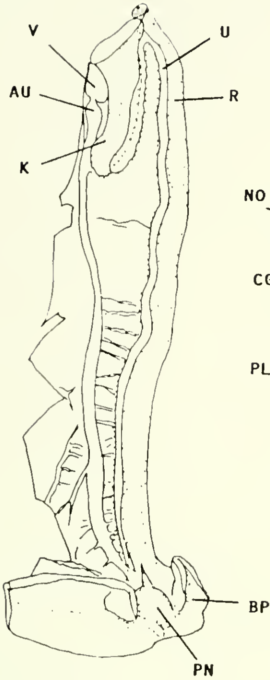


348

FIGS. 349–355: SUBULINIDAE, ACHATINIDAE
349) *Rumina decollata,* pulmonary complex. 7.9mm.
350) *Rumina decollata,* digestive tract. 7.9mm.
351) *Rumina decollata,* nervous system in dorsal view. 3.25mm.
352) *Idem,* cerebral commissure cut. 3.25mm.
353) *Achatina fulica,* digestive tract. 1.9mm.
354) *Achatina fulica,* nervous system in dorsal view. 5mm.
355) *Idem,* cerebral commissure cut. 5mm.

349



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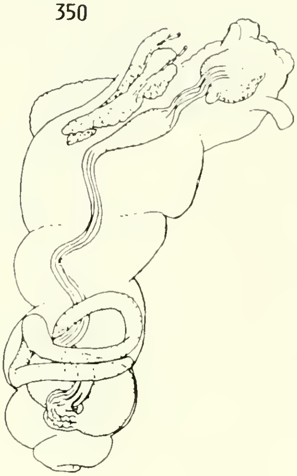

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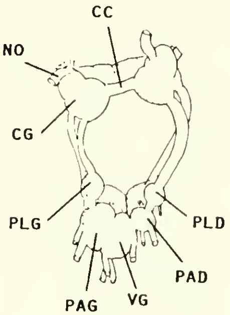

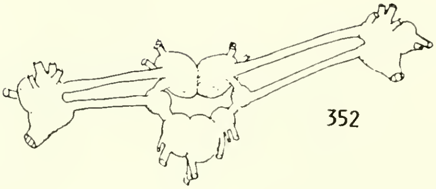

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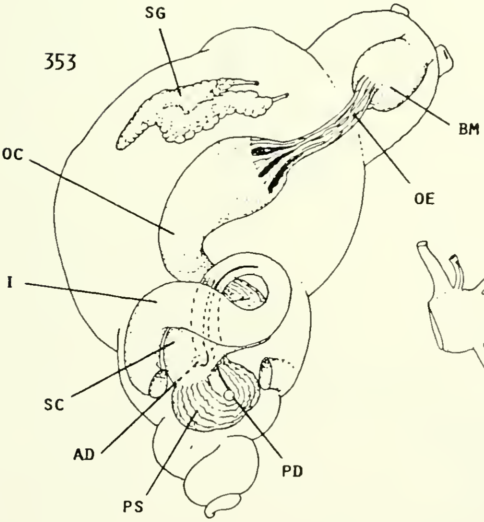

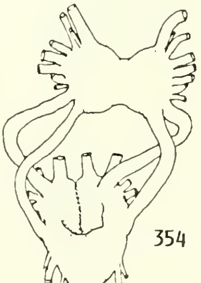

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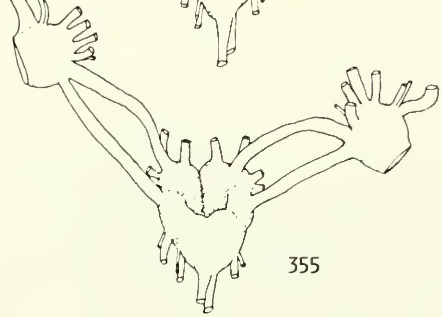
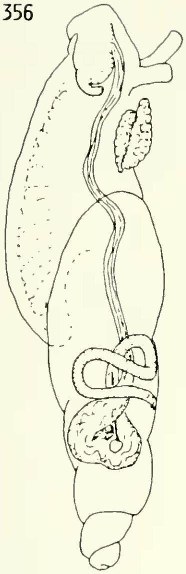


355

FIGS. 356–363: FERUSSACIIDAE, OLEACINIDAE
356) *Cecilioides acicula*, digestive tract. 2mm.
357) *Poiretia dilatata*, digestive tract. 5.8mm.
358) *Cecilioides acicula*, pulmonary complex. 2mm.
359) *Cecilioides acicula*, nervous system in dorsal view. 1.3mm.
360) *Idem*, cerebral commissure cut. 1.3mm.
361) *Poiretia dilatata*, pulmonary complex seen from outside. 5.8mm.
362) *Poiretia dilatata*, nervous system in dorsal view. 3.6mm.
363) *Idem*, cerebral commissure cut. 3.6mm.

356



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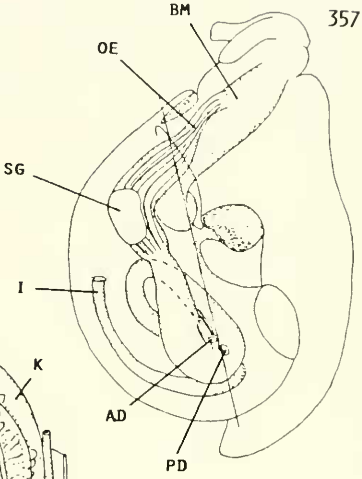

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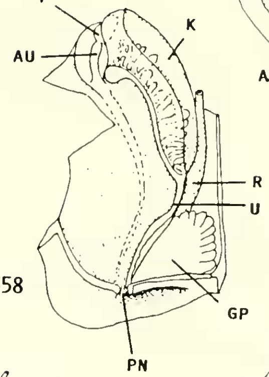

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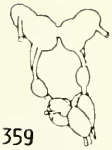

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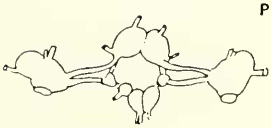

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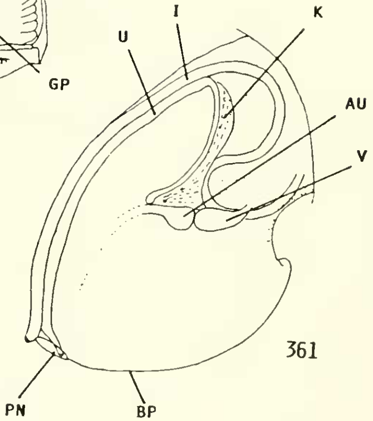

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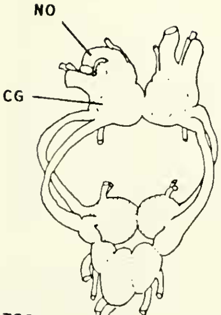

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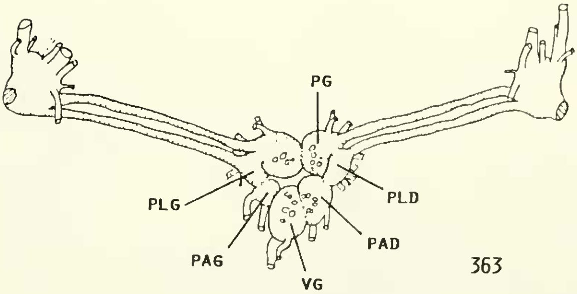
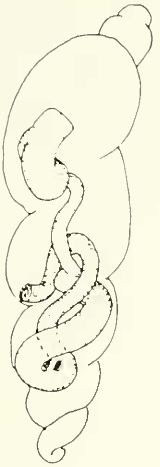


FIGS. 364–371: OLEACINIDAE
364) *Spiraxis futilis*, digestive tract. 1.4mm.
365) *Varicella biplicata*, digestive tract. 9mm.
366) *Varicella biplicata*, pulmonary complex. 4.4mm.
367) *Varicella biplicata*, kidney internal morphology. 4.4mm.
368) *Varicella biplicata*, nervous system in dorsal view. 2mm.
369) *Varicella biplicata*, right lateral view of nervous system. 2mm.
370) *Varicella biplicata*, nervous system in dorsal view, cerebral commissure cut. 1mm.
371) *Euglandina carminensis*, digestive tract. ca. 14mm.

364



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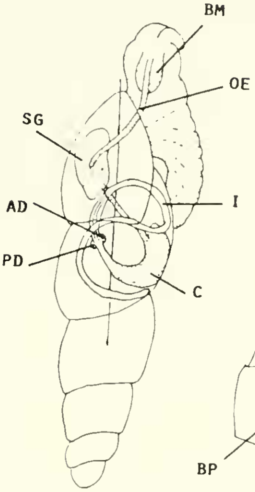

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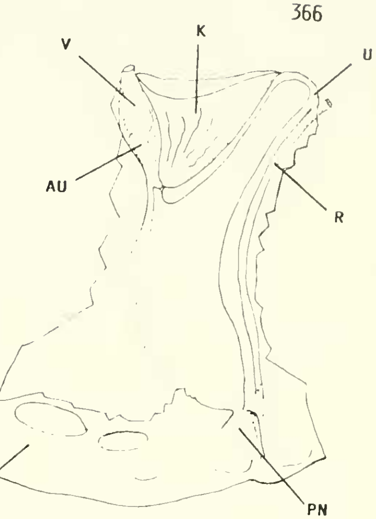

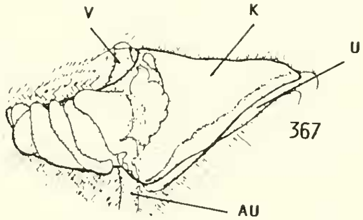

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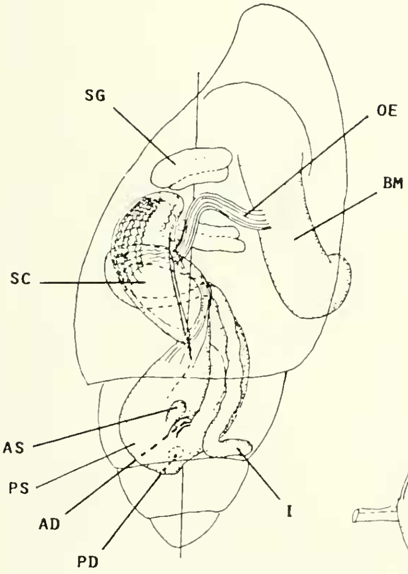

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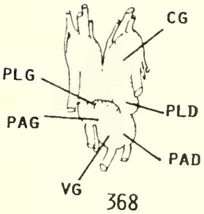

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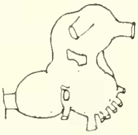

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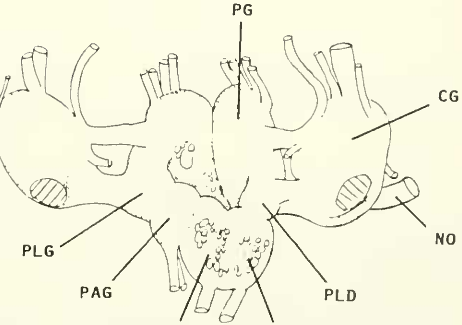
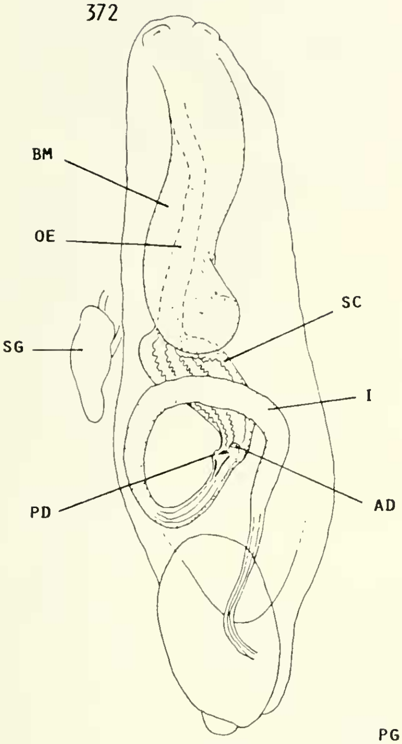


370

FIGS. 372–379: OLEACINIDAE, RHYTIDIDAE
372) *Strebelia berendti,* digestive tract. 4.5mm.
373) *Strebelia berendti,* nervous system in dorsal view. 2mm.
374) *Idem,* cerebral commissure cut. 2mm.
375) *Priodiscus serratus,* digestive tract. 2.3mm.
376) *Priodiscus serratus,* nervous system in dorsal view, cerebral commissure cut. 1mm.
377) *Priodiscus serratus,* nervous system in dorsal view. 1mm.
378) *Priodiscus serratus,* pulmonary complex. 2.3mm.
379) *Priodiscus serratus,* genital apparatus. 1.9mm.

372



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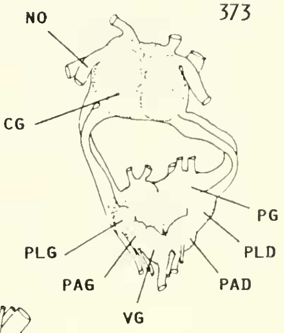

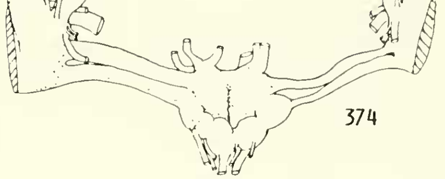

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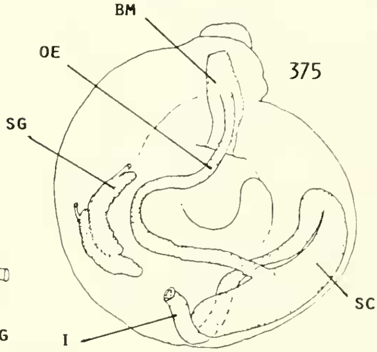

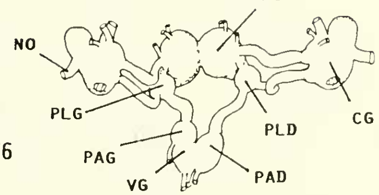

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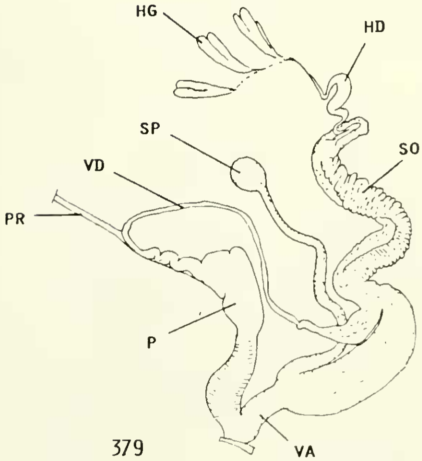

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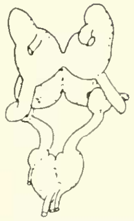

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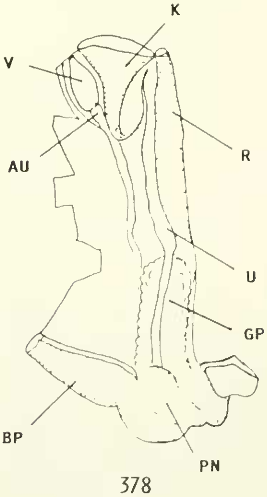
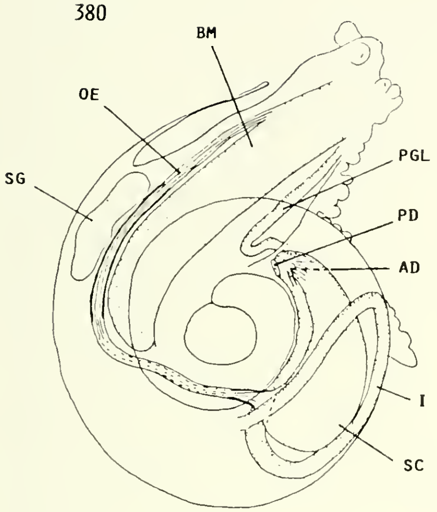


378

FIGS. 380–387: RHYTIDIDAE
380) *Rhytida inaequalis*, digestive tract. 11.9mm.
381) *Nata vernicosa*, digestive tract. 5mm.
382) *Nata vernicosa*, pulmonary complex. 7mm.
383) *Nata vernicosa*, kidney internal morphology. 4.1mm.
384) *Nata vernicosa*, nervous system in dorsal view. 2.1mm.
385) *Idem*, cerebral commissure cut. 2.1mm.
386) *Ouagapia raynali*, nervous system in dorsal view. 5mm.
387) *Idem*, cerebral commissure cut. 5mm.

380



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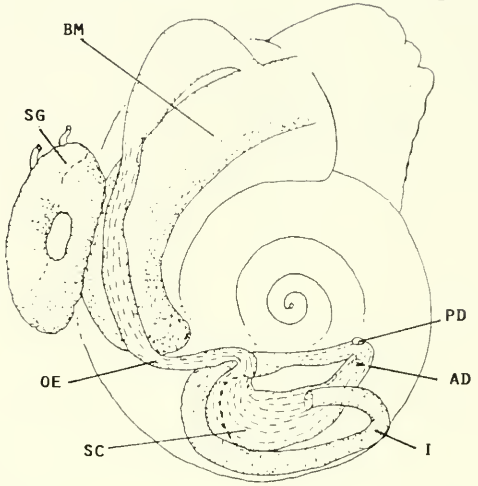

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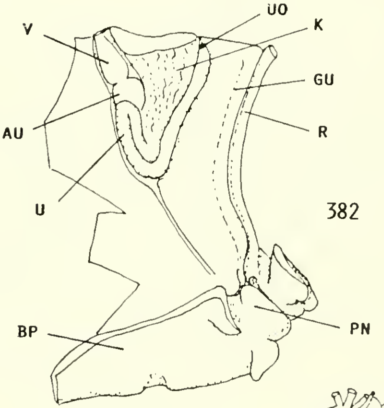

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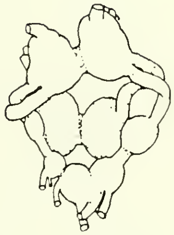

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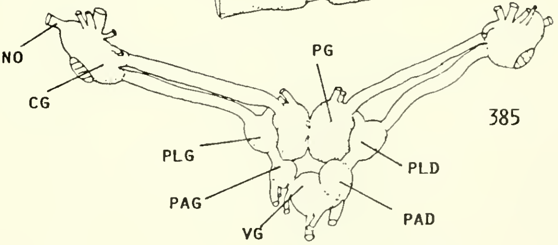

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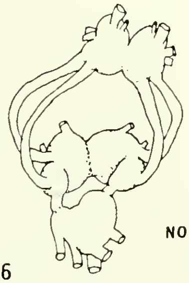

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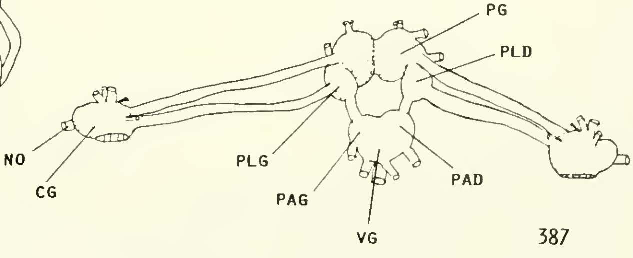
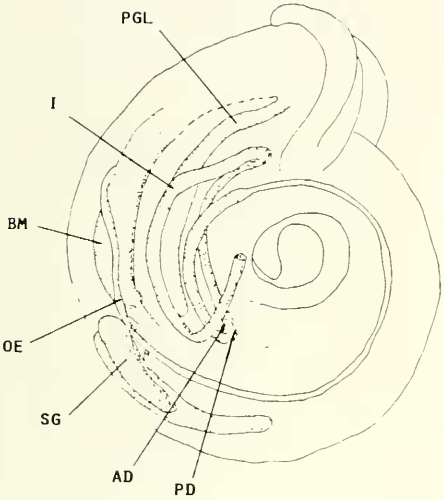


FIGS. 388–393: RHYTIDIDAE
388) *Diplomphalus megei*, digestive tract. 6.5mm.
389) *Diplomphalus megei*, pulmonary complex. 6.5mm.
390) *Diplomphalus megei*, nervous system in dorsal view. 2mm.
391) *Idem*, cerebral commissure cut. 2mm.
392) *Chlamydephorus gibbonsi*, digestive tract. 1.5mm.
393) *Schizoglossa novoseelandica*, digestive tract. 10mm.

388



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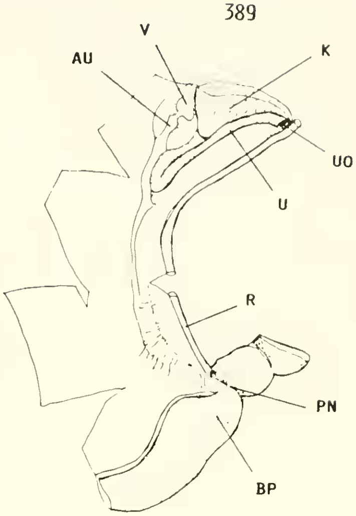

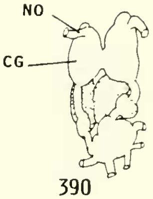

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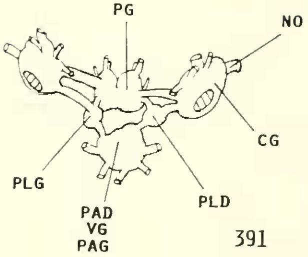

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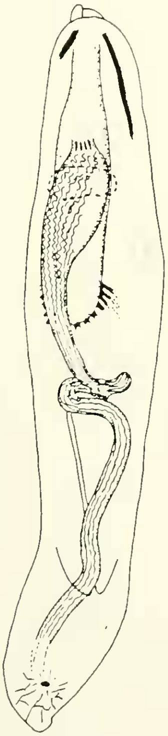

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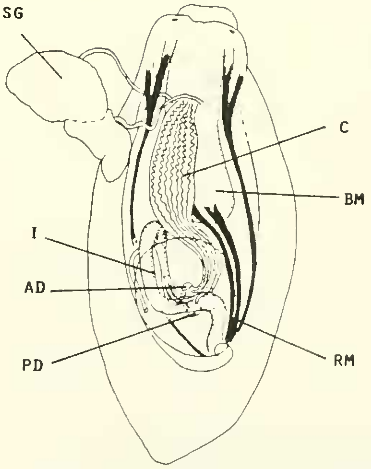
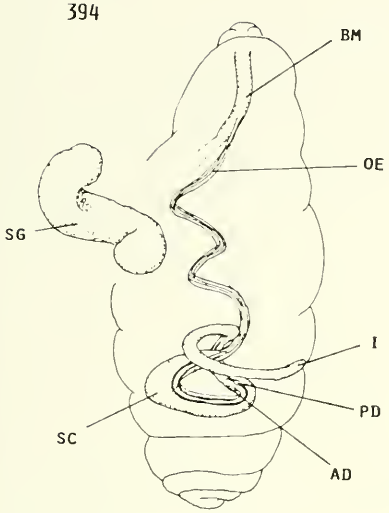
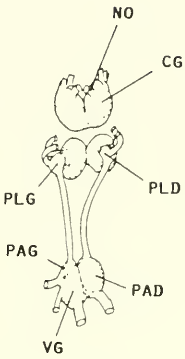


393

FIGS. 394–398: STREPTAXIDAE
394) *Ptychotrema* sp., digestive tract. 5.9mm.
395) *Ptychotrema* sp., pulmonary complex. 10mm.
396) *Ptychotrema* sp., nervous system in dorsal view. 1.9mm.
397) *Edentulina* sp., digestive tract. 10mm.
398) *Edentulina* sp., pulmonary complex. 10mm.

394





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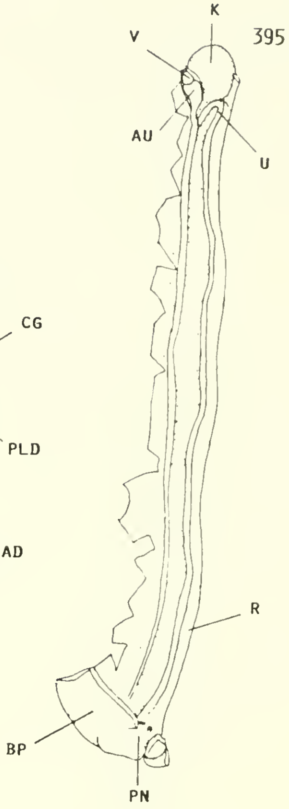

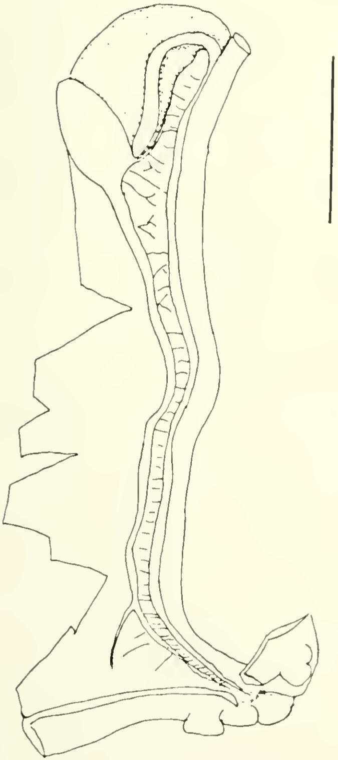

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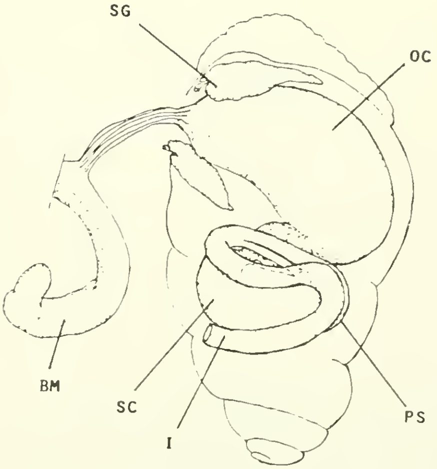
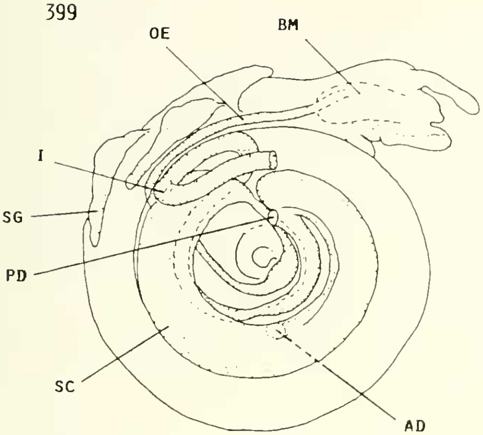


397

FIGS. 399–405: SYSTROPHIIDAE
399) *Systrophia eudiscus*, digestive tract. 6.8mm.
400) *Systrophia eudiscus*, nervous system in dorsal view. 2mm.
401) *Idem*, cerebral commissure cut. 2mm.
402) *Systrophia eudiscus*, pulmonary complex. 11.3mm.
403) *Systrophia eudiscus*, kidney internal morphology. 4mm.
404) *Tamayoa decolorata*, digestive tract. 3.1mm.
405) *Systrophia (Wayampia) cayennensis*, digestive tract. 4mm.

399



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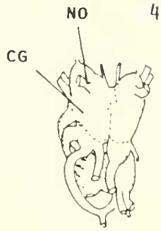

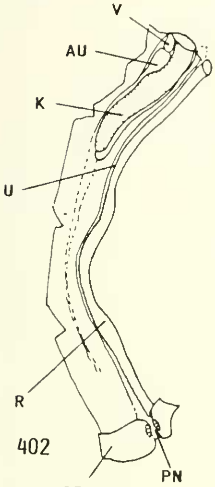

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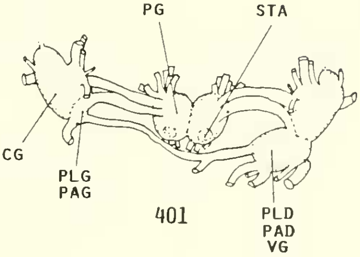

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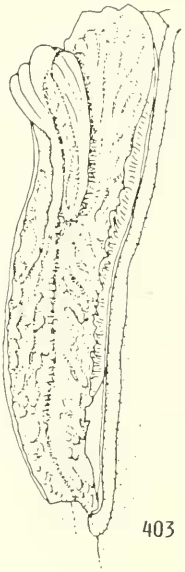

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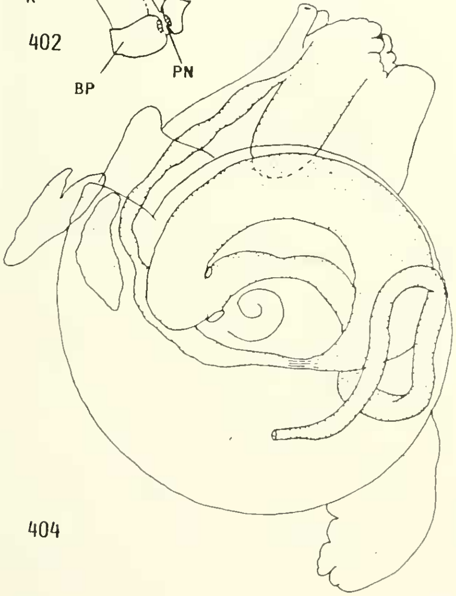

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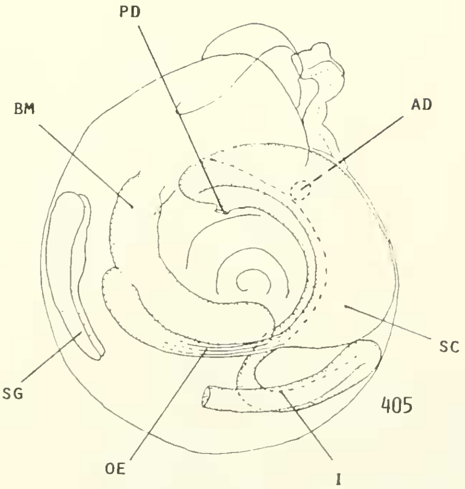
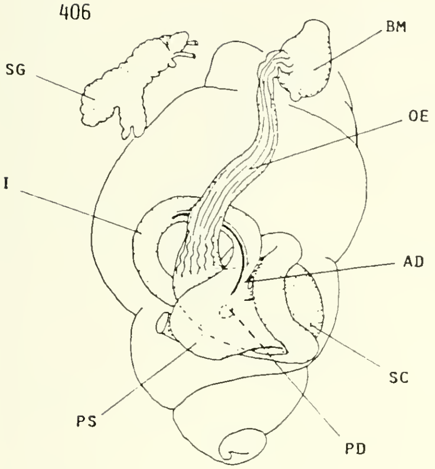


405

FIGS. 406–411: ACAVIDAE (Australia)
406) *Caryodes* sp., digestive tract. 10mm.
407) *Caryodes* sp., nervous system in dorsal view. 3mm.
408) *Idem,* cerebral commissure cut. 3mm.
409) *Panda larreyi,* digestive tract. 1.5mm.
410) *Panda larreyi,* nervous system in dorsal view. 5mm.
411) *Idem,* cerebral commissure cut. 5mm.

406



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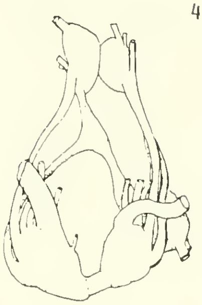

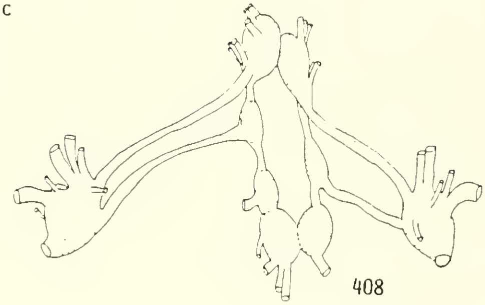

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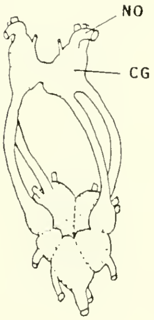

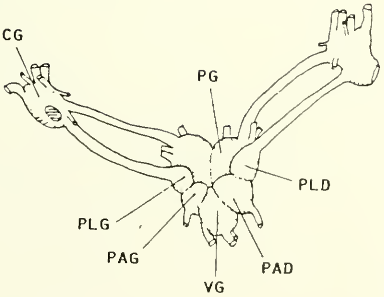

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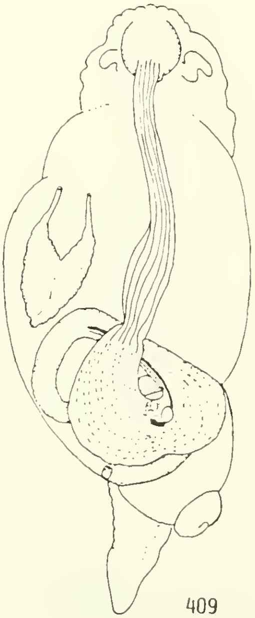
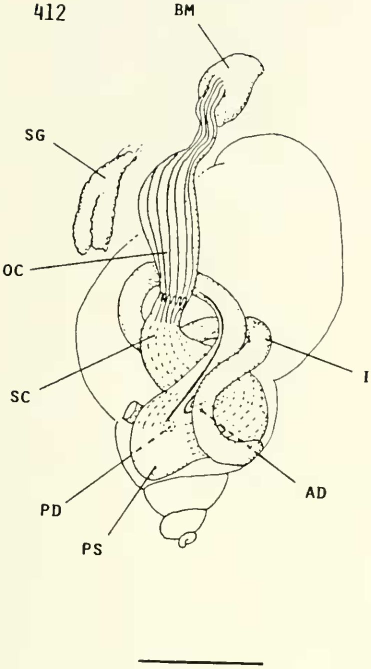


409

FIGS. 412–416: ACAVIDAE (Australia)
412) *Pygmipanda kershawi*, digestive tract. 2cm.
413) *Pygmipanda kershawi*, nervous system in dorsal view. 2.3mm.
414) *Idem*, cerebral commissure cut. 2.3mm.
415) *Pygmipanda kershawi*, pulmonary complex. 2cm.
416) *Pygmipanda kershawi*, kidney internal morphology. 7mm.

412



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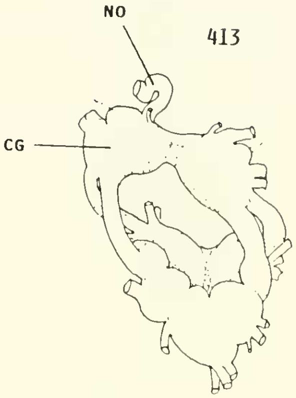

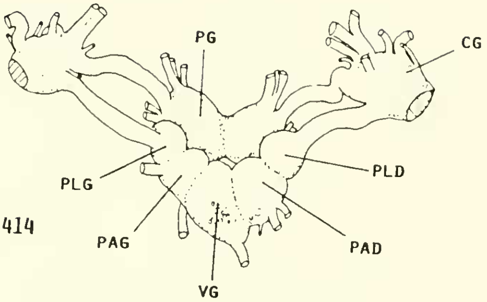

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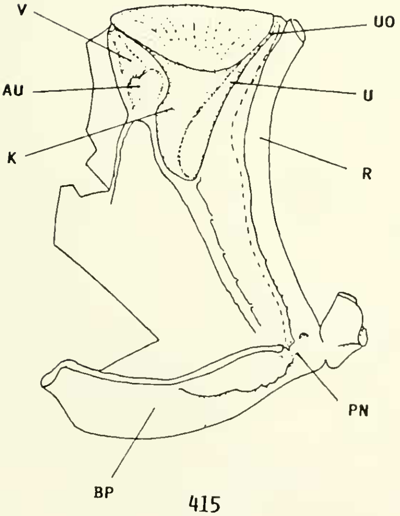

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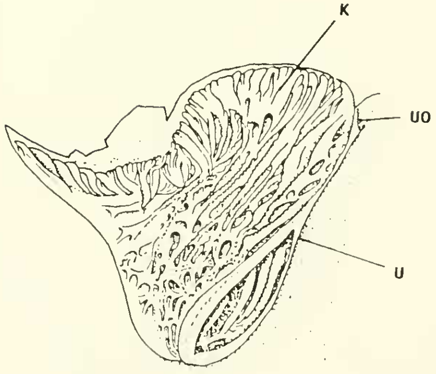
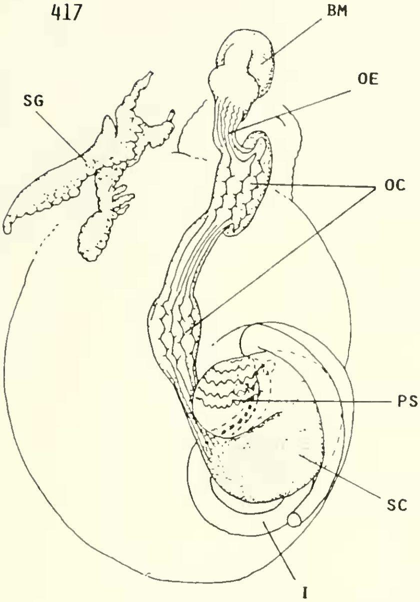


416

FIGS. 417–422: ACAVIDAE (Australia)
417) *Hedleyella falconeri*, digestive tract. 2cm.
418) *Pandofella whitei*, digestive tract. 1cm.
419) *Pandofella whitei*, nervous system in dorsal view. 3.25mm.
420) *Idem*, cerebral commissure cut. 3.25mm.
421) *Hedleyella falconeri*, nervous system in dorsal view. 4.2mm.
422) *Idem*, cerebral commissure cut. 4.2mm.

417



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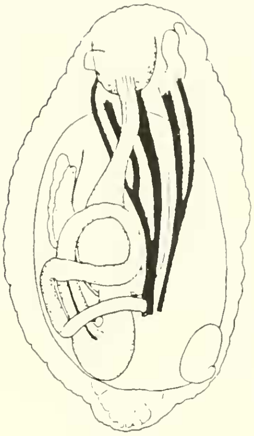

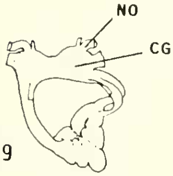

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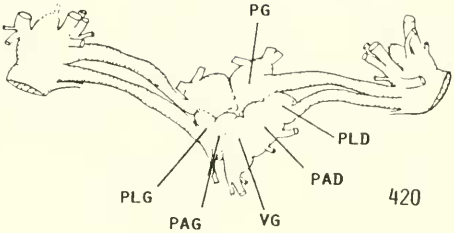

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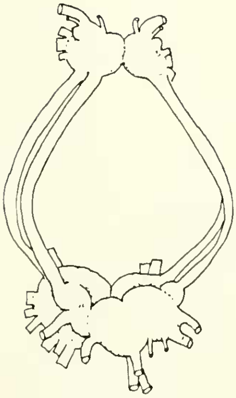

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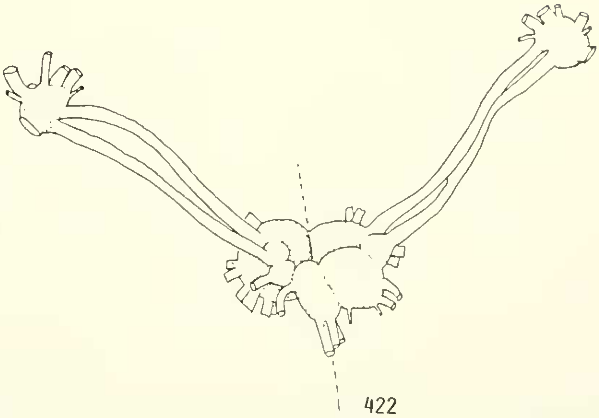
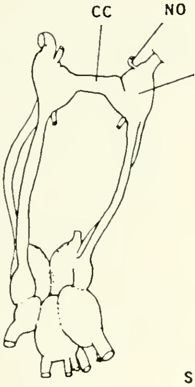


422

FIGS. 423–427: ACAVIDAE (Australia)
423) *Pedinogyra* sp., nervous system in dorsal view. 4mm.
424) *Idem,* cerebral commissure cut. 4mm.
425) *Pedinogyra* sp., digestive tract. 1.7cm.
426) *Pedinogyra* sp., kidney internal morphology. 8mm.
427) *Pedinogyra* sp., pulmonary complex. 2.9cm.

423



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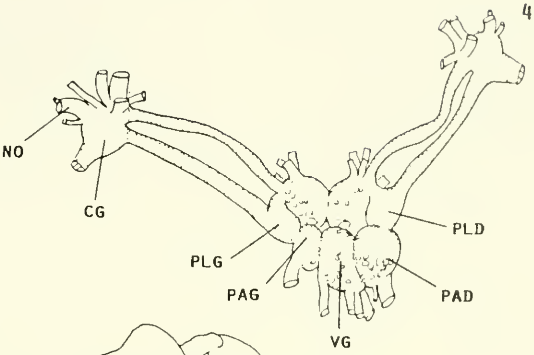

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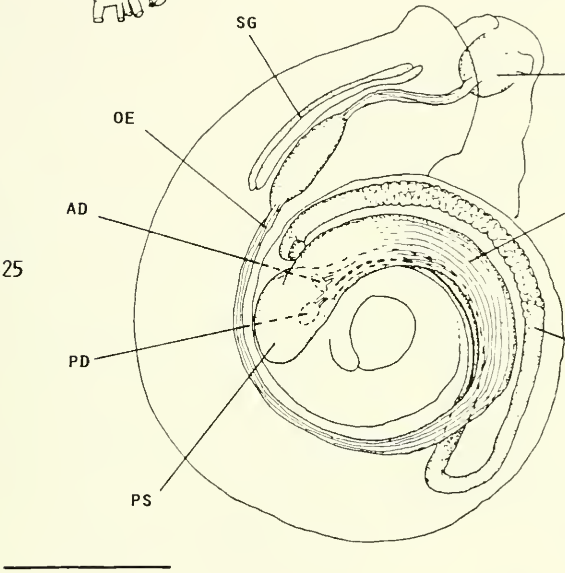

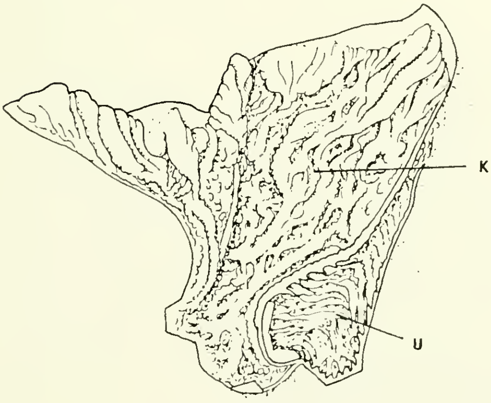

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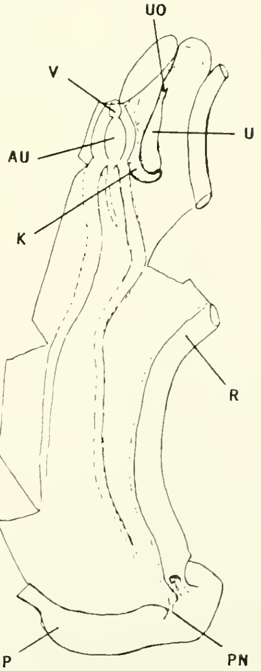
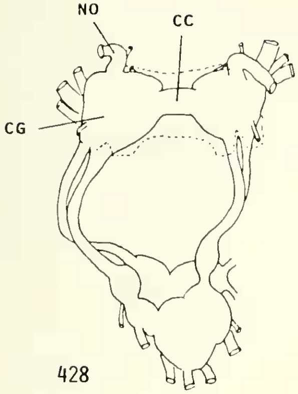


427

FIGS. 428–432: ACAVIDAE (South Africa)
428) *Dorcasia alexandri,* nervous system in dorsal view. 2mm.
429) *Idem,* cerebral commissure cut. 2mm.
430) *Dorcasia alexandri,* digestive tract. 7.8mm.
431) *Dorcasia alexandri,* pulmonary complex. 22.5mm.
432) *Dorcasia alexandri,* kidney internal morphology. 4.2mm.



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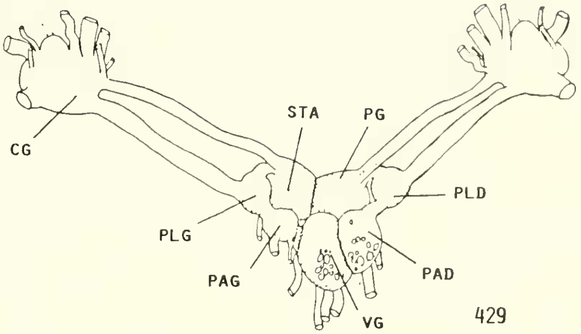

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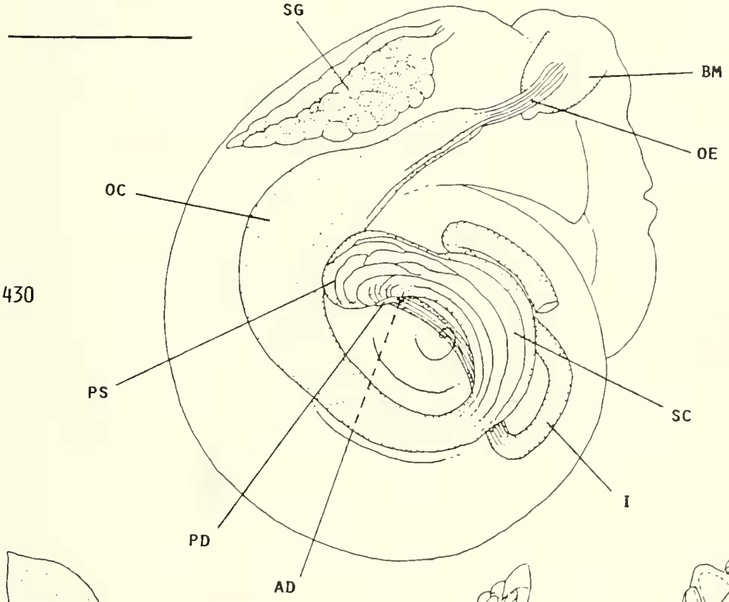

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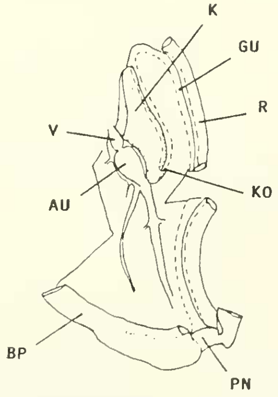

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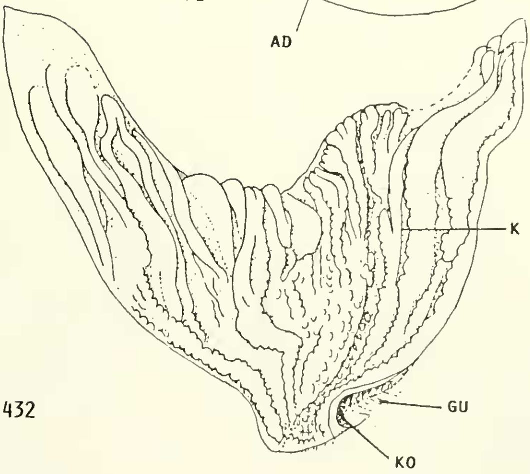
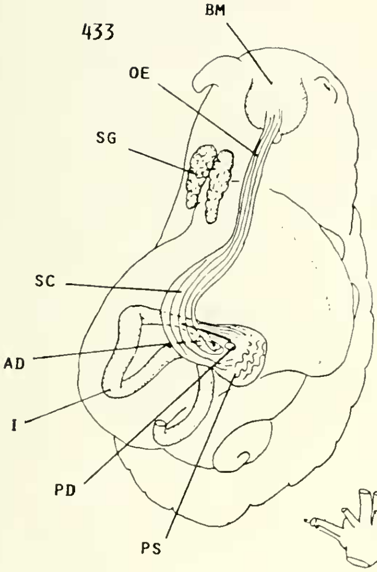


432

FIGS. 433–439: ACAVIDAE (South Africa, South America)
433) *Trigonephrus rosaceus*, digestive tract. 12mm.
434) *Trigonephrus rosaceus*, nervous system in dorsal view. 3.25mm.
435) *Idem*, cerebral commissure cut. 3.25mm.
436) *Macrocyclis laxata*, digestive tract. 2cm.
437) *Macrocyclis laxata*, nervous system in dorsal view. 6mm.
438) *Idem*, cerebral commissure cut. 6mm.
439) *Macrocyclis laxata*, kidney internal morphology. 6mm.

433



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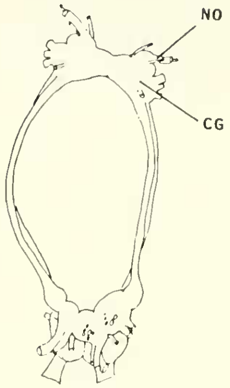

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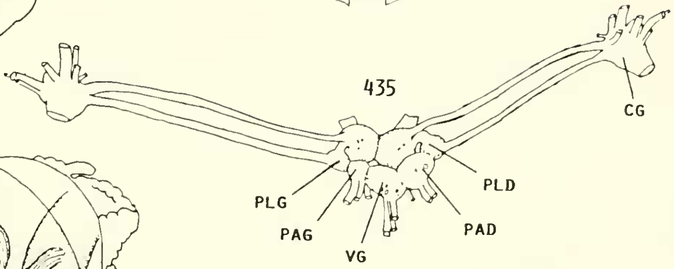

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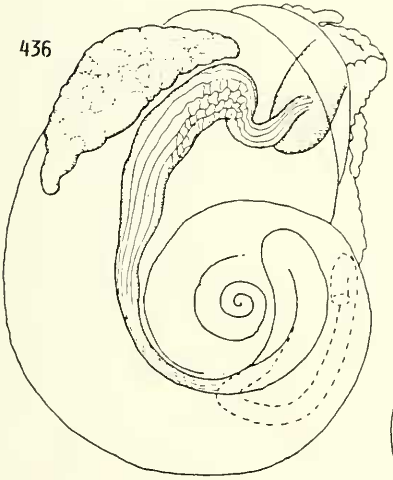

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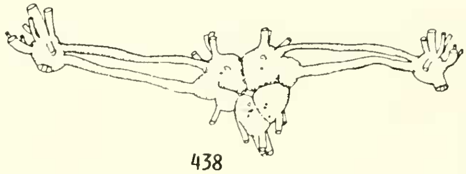

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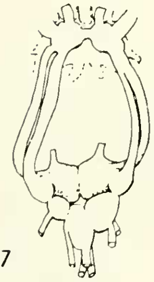

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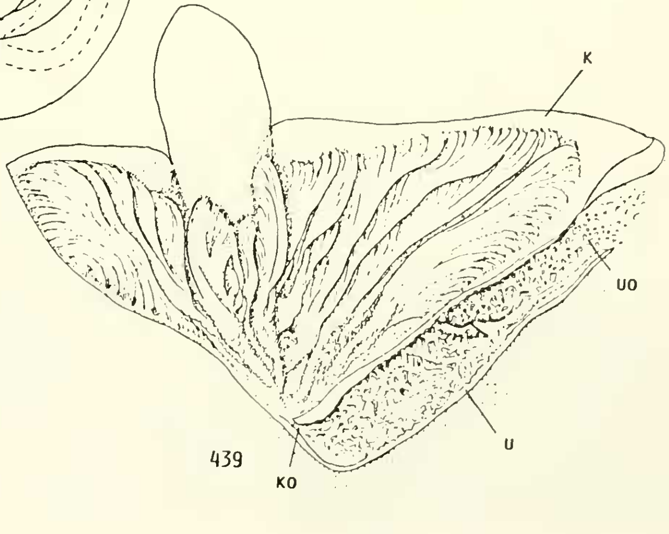
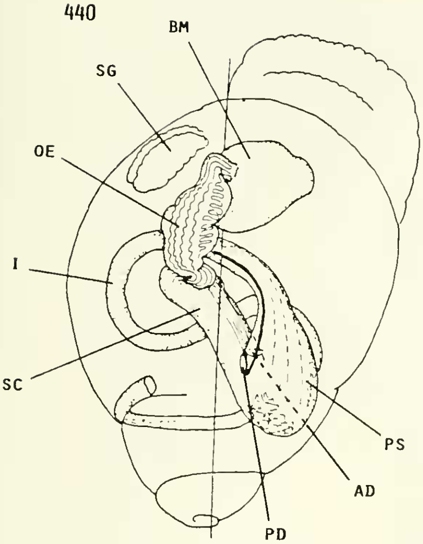
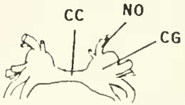


FIGS. 440–449: ACAVIDAE (South America, Seychelles)
440) *Strophocheilus chilensis*, digestive tract. 6mm.
441) *Strophocheilus chilensis*, cerebral ganglia in dorsal view, sheath dissected. 3mm.
442) *Strophocheilus chilensis*, nervous system in dorsal view, sheath intact. 3mm.
443) *Idem*, cerebral commissure cut. 3mm.
444) *Idem*, cerebral commissure cut, conjunctive sheath dissected. 3mm.
445) *Strophocheilus chilensis*, pulmonary complex. 8.6mm.
446) *Strophocheilus chilensis*, kidney internal morphology. 3mm.
447) *Stylodon studerianus*, digestive tract. 17mm.
448) *Stylodon studerianus*, nervous system in dorsal view. 3.3mm.
449) *Idem*, cerebral commissure cut. 3.3mm.

440





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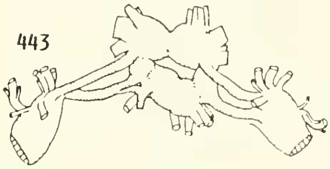

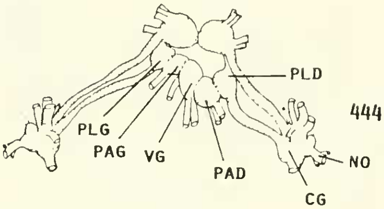

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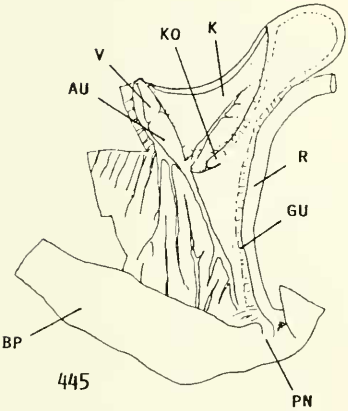

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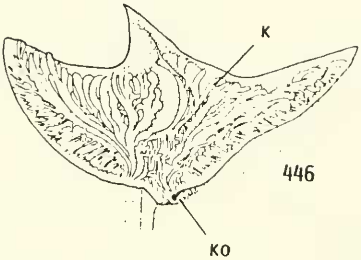

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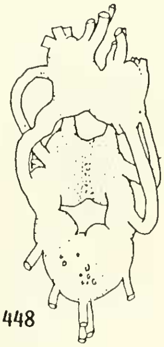

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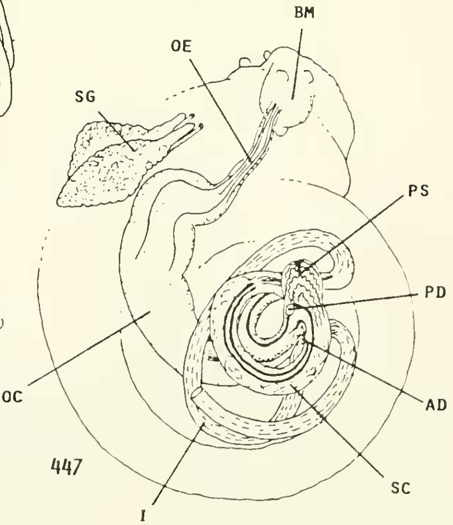

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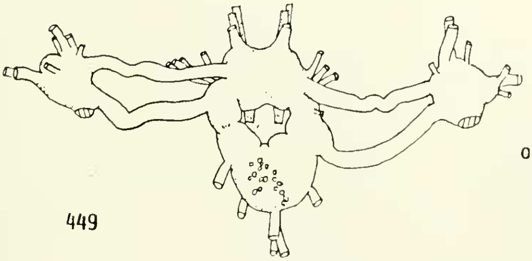
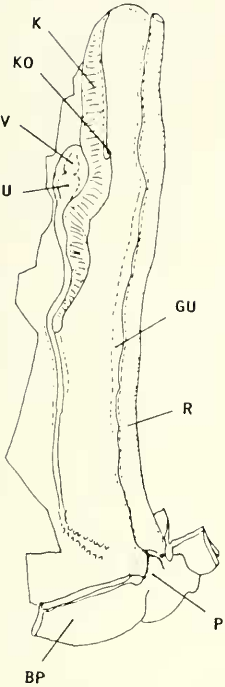


449

FIGS. 450–456: ACAVIDAE (Seychelles, Madagascar)
450) *Stylodon studerianus,* pulmonary complex. 4.5cm.
451) *Stylodon studerianus,* kidney internal morphology. 2cm.
452) *Ampelita petiti,* pulmonary complex. 2.25cm.
453) *Ampelita petiti,* kidney internal morphology. 6.4mm.
454) *Ampelita petiti,* digestive tract. 10.6mm.
455) *Ampelita petiti,* nervous system in dorsal view, cerebral commissure cut. 3.5mm.
456) *Ampelita petiti,* nervous system in dorsal view. 3.5mm.

450



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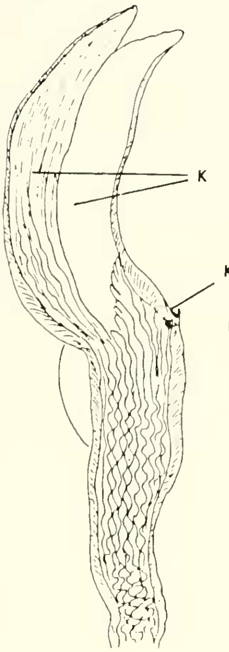

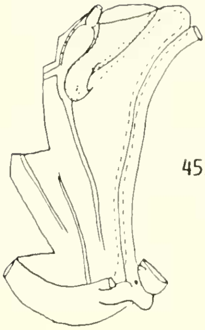

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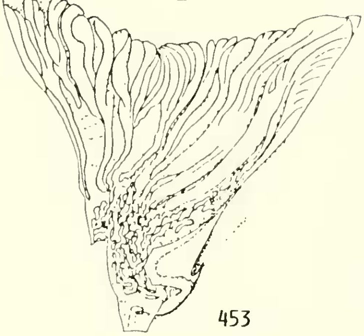

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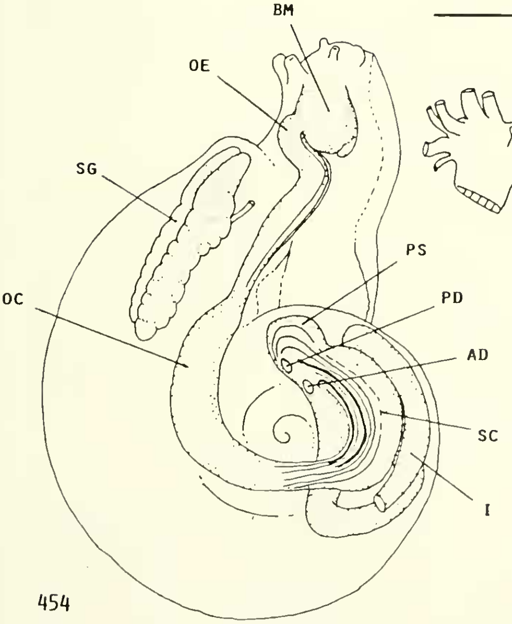

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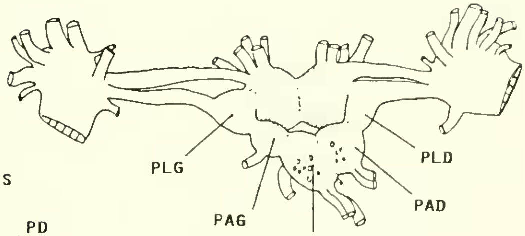

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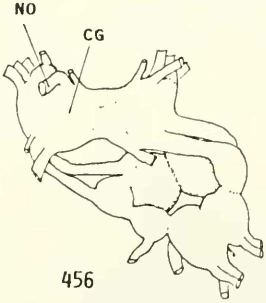
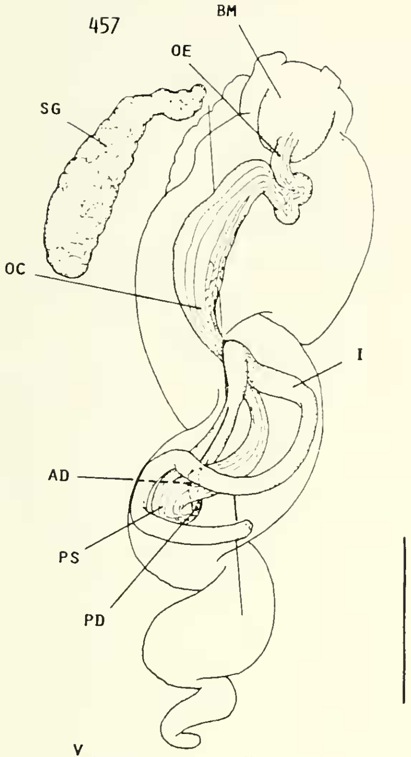


456

FIGS. 457–464: ACAVIDAE (Madagascar)
457) *Clavator eximius,* digestive tract. 1.6cm.
458) *Clavator eximius,* nervous system in dorsal view. 4mm.
459) *Idem,* cerebral commissure cut. 4mm.
460) *Helicophanta vesicalis,* nervous system in dorsal view. 4mm.
461) *Idem,* cerebral commissure cut. 4mm.
462) *Clavator eximius,* pulmonary complex. 2.5cm.
463) *Clavator eximius,* kidney internal morphology. 8mm.
464) *Helicophanta vesicalis,* digestive tract. 2.3cm.

457



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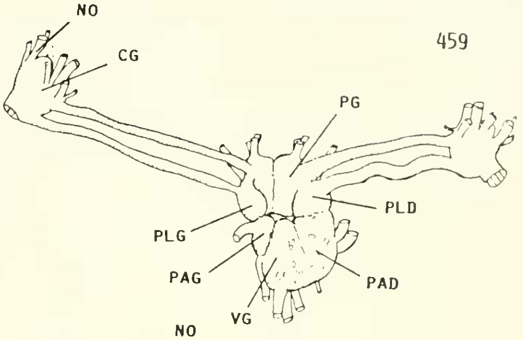

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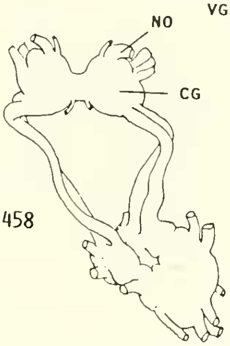

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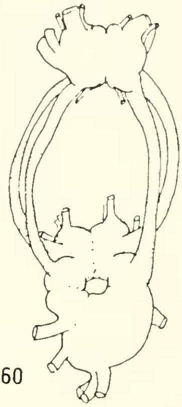

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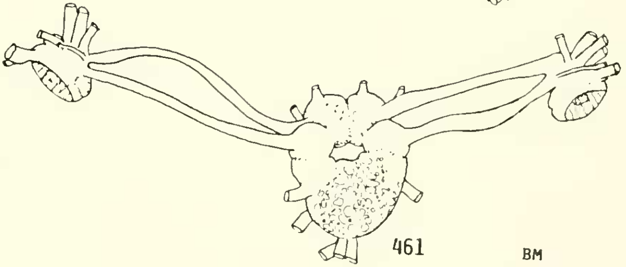

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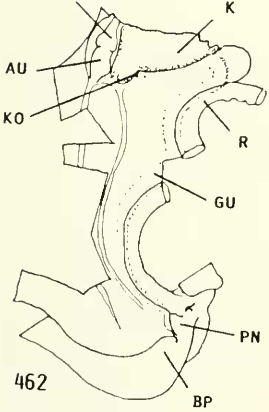

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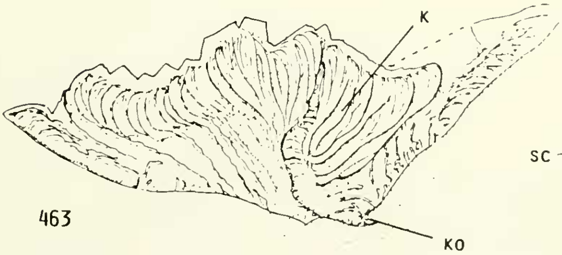

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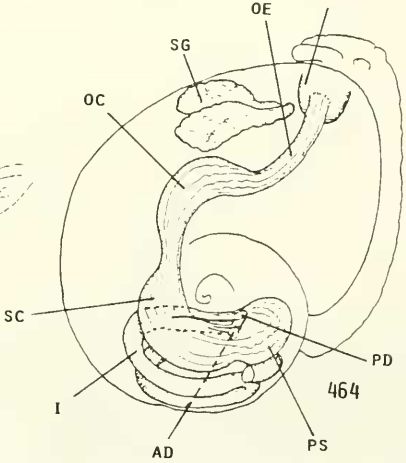
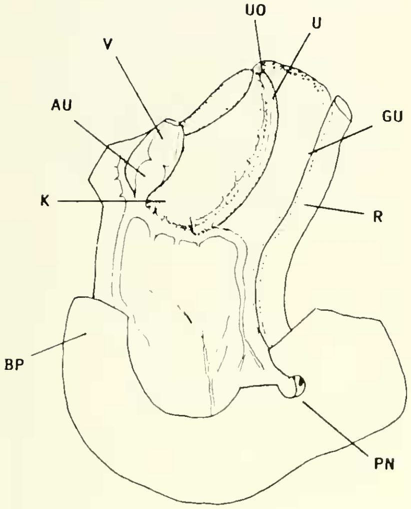


FIGS. 465–469: ACAVIDAE (Madagascar, Ceylon)
465) *Helicophanta vesicalis,* pulmonary complex. 1.6cm.
466) *Helicophanta vesicalis,* kidney internal morphology. 8mm.
467) *Acavus superbus,* digestive tract. 1.6cm.
468) *Acavus superbus,* nervous system in dorsal view. 6.1mm.
469) *Idem,* cerebral commissure cut. 6.1mm.

465



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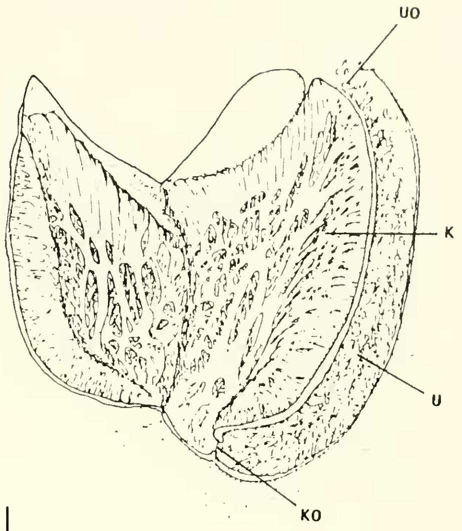

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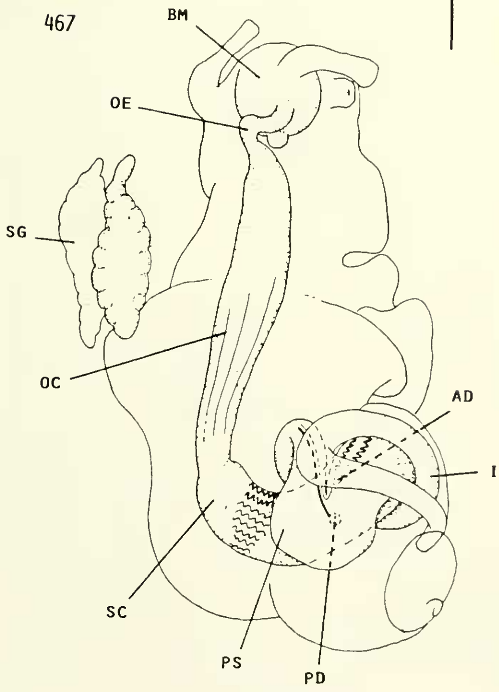

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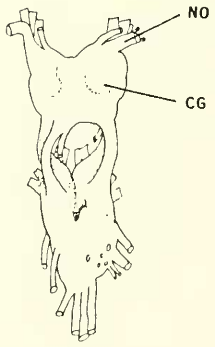
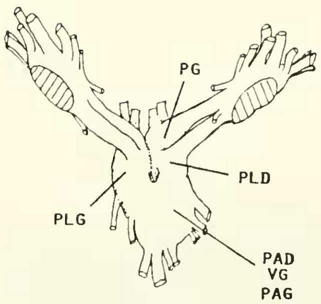
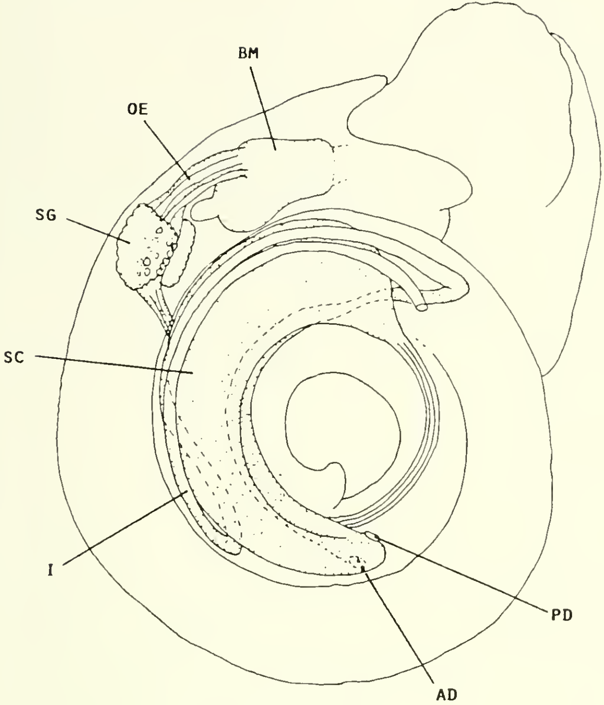




469

FIGS. 470–475: CORILLIDAE
470) *Sculptaria collaris*, digestive tract. 2mm.
471) *Sculptaria collaris*, pulmonary complex. 4.75mm.
472) *Sculptaria collaris*, kidney internal morphology. 1.9mm.
473) *Sculptaria collaris*, nervous system in dorsal view. 0.8mm.
474) *Idem*, cerebral commissure cut. 0.8mm.
475) *Sculptaria collaris*, genital apparatus. 3mm.

470



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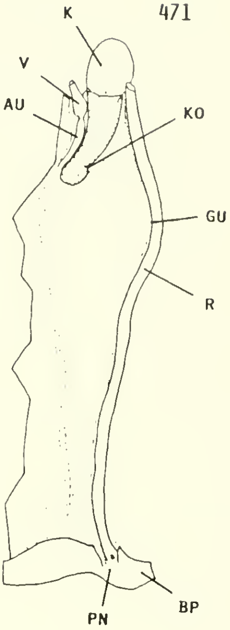

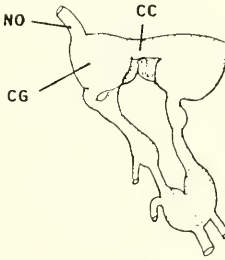

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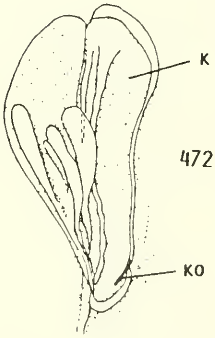

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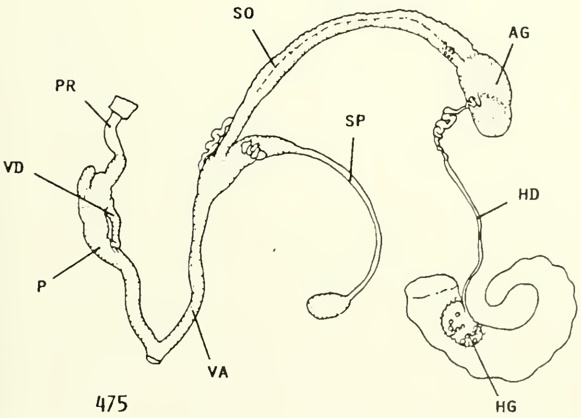

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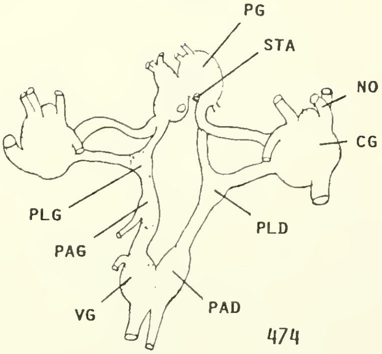
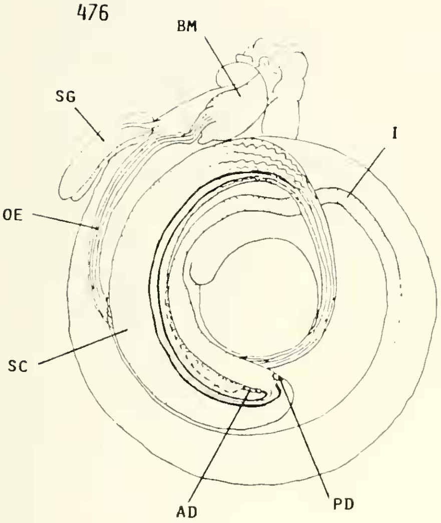


474

FIGS. 476–485: CORILLIDAE
476) *Craterodiscus pricei*, digestive tract. 2mm.
477) *Craterodiscus pricei*, right lateral view of central nervous system. 1mm.
478) *Craterodiscus pricei*, nervous system in dorsal view. 1mm.
479) *Idem*, cerebral commissure cut. 1mm.
480) *Craterodiscus pricei*, kidney internal morphology. 1mm.
481) *Plectopylis* sp., digestive tract. 5mm.
482) *Plectopylis* sp., pulmonary complex. 8mm.
483) *Plectopylis* sp., nervous system in dorsal view. 2mm.
484) *Idem*, cerebral commissure cut. 2mm.
485) *Plectopylis* sp., kidney internal morphology. 3.1mm.

476



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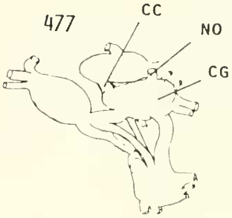

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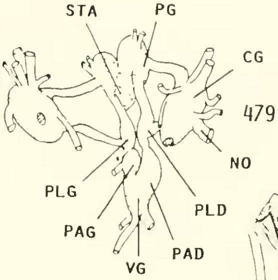

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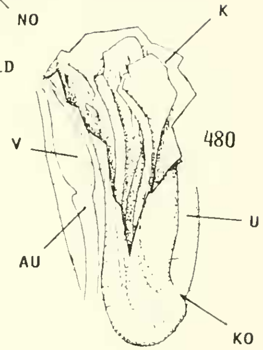

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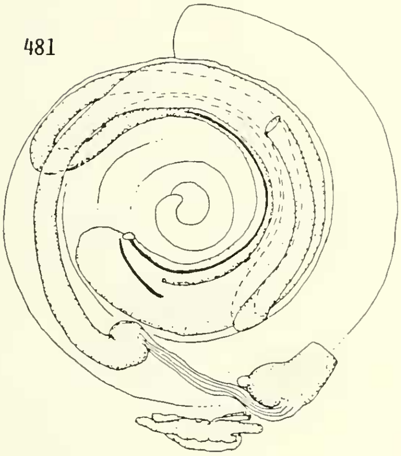

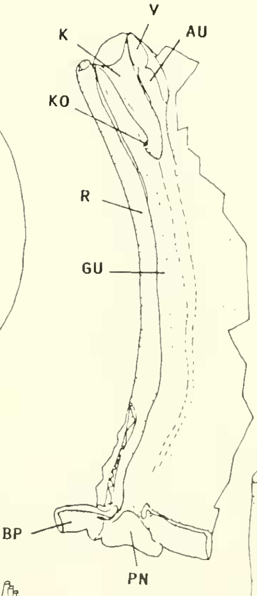

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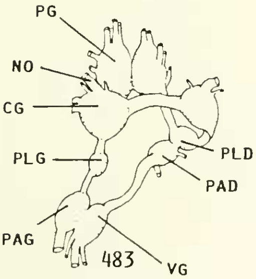

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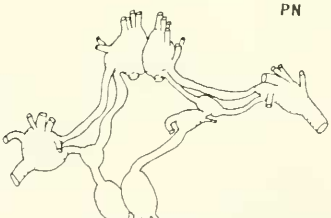

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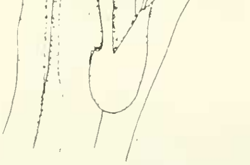
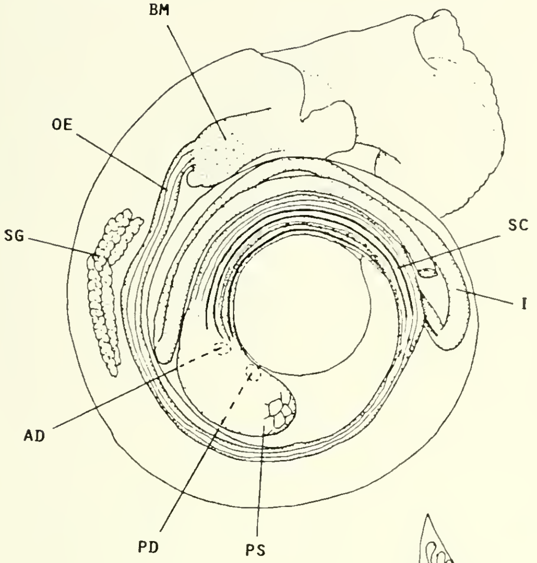


485

FIGS. 486–491: CORILLIDAE
486) *Corilla humberti*, digestive tract. 6.4mm.
487) *Corilla humberti*, nervous system in dorsal view. 1.4mm.
488) *Idem*, cerebral commissure cut. 2mm.
489) *Corilla humberti*, pulmonary complex. 10mm.
490) *Corilla humberti*, kidney internal morphology. 3.8mm.
491) *Corilla humberti*, genital apparatus. 10mm.

486



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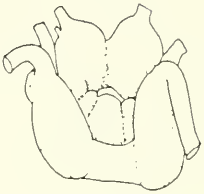

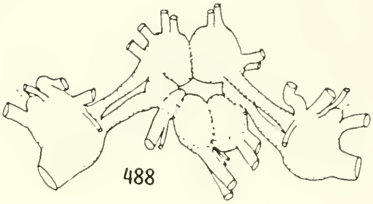

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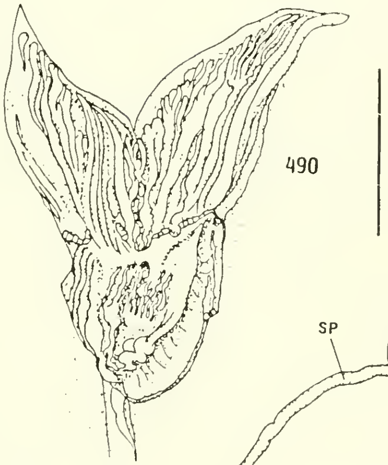

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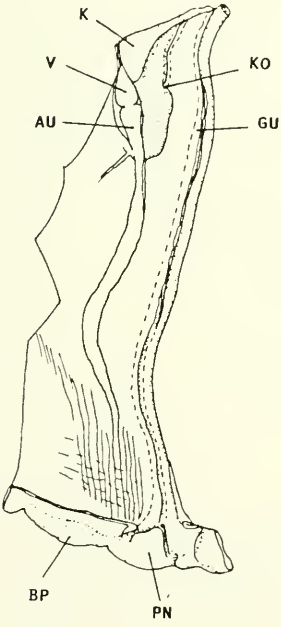

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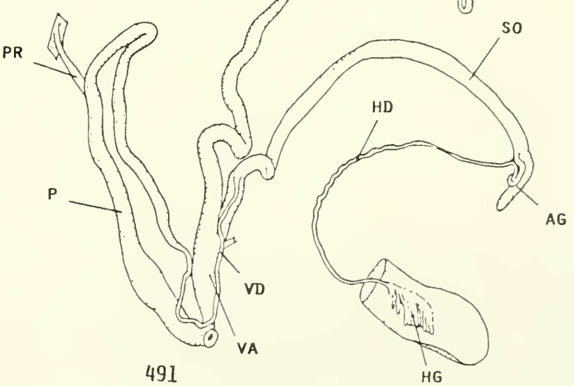
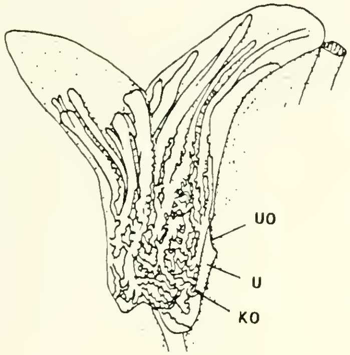


491

FIGS. 492–499: OREOHELICIDAE (OREOHELICINAE, AMMONITELLINAE)
492) *Oreohelix barbata,* digestive tract. 5mm.
493) *Oreohelix barbata,* kidney internal morphology. 3.7mm.
494) *Oreohelix barbata,* pulmonary complex. 8.5mm.
495) *Oreohelix barbata,* nervous system in dorsal view. 2mm.
496) *Idem,* cerebral commissure cut. 2mm.
497) *Ammonitella yatesi,* digestive tract. 3.7mm.
498) *Ammonitella yatesi,* nervous system in dorsal view. 1.5mm.
499) *Idem,* cerebral commissure cut. 1.5mm.

493



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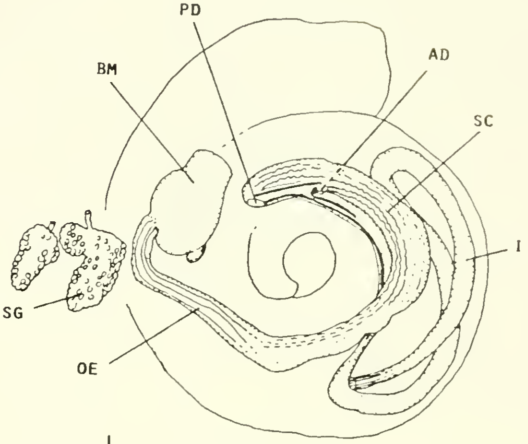

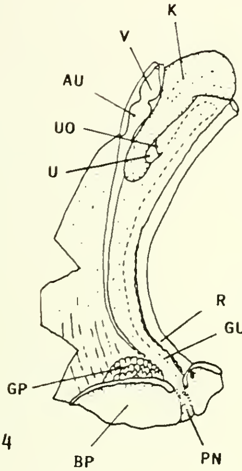

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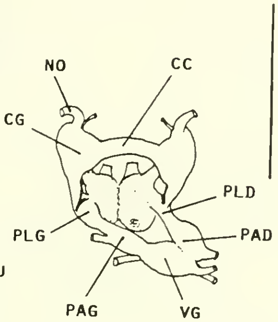

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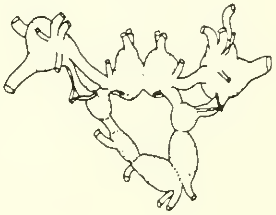

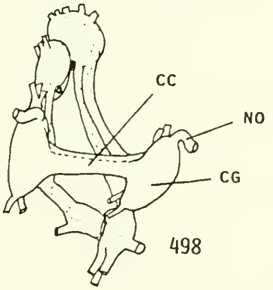

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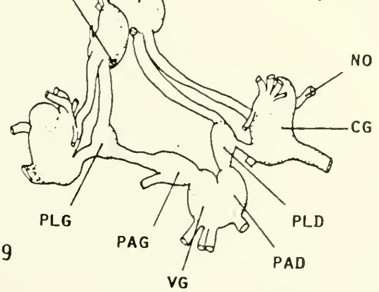

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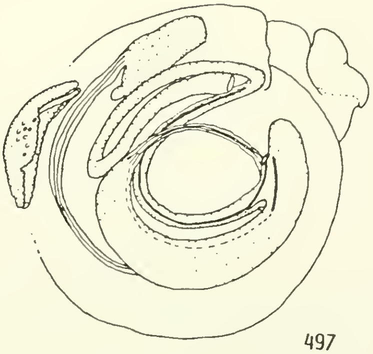
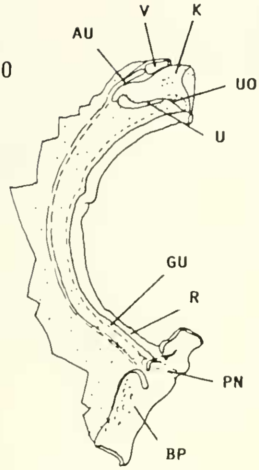


497

FIGS. 500–504: OREOHELICIDAE (AMMONITELLINAE)
500) *Ammonitella yatesi,* pulmonary complex. 6.3mm.
501) *Ammonitella yatesi,* kidney internal morphology. 2.5mm.
502) *Glyptostoma gabrielense,* digestive tract. 10.3mm.
503) *Glyptostoma gabrielense,* nervous system in dorsal view. 2.5mm.
504) *Idem,* cerebral commissure cut. 2.5mm.

500



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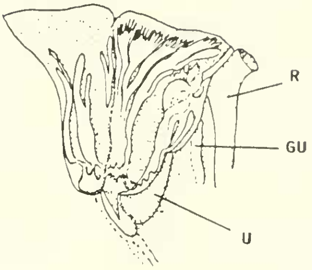

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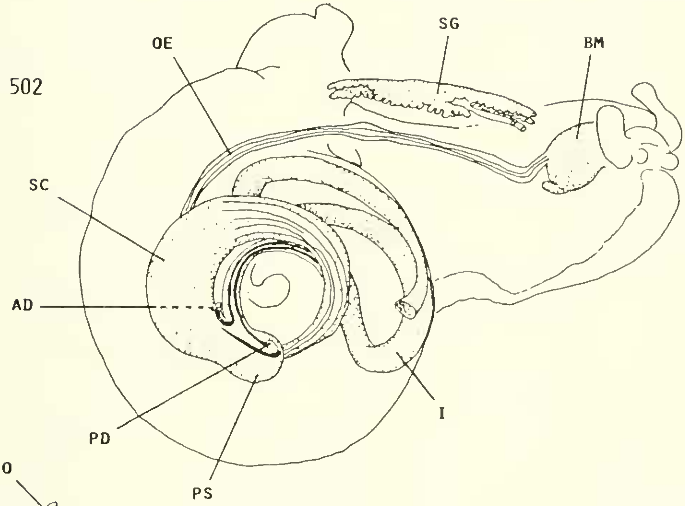

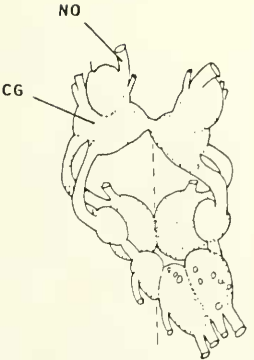

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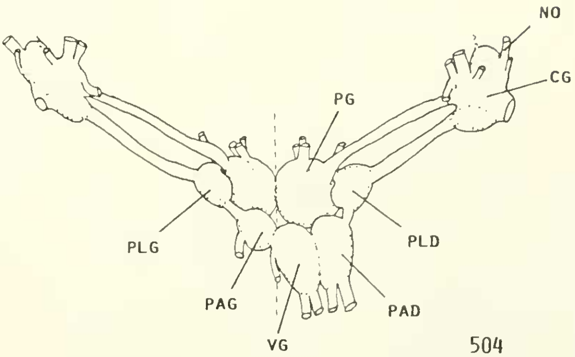
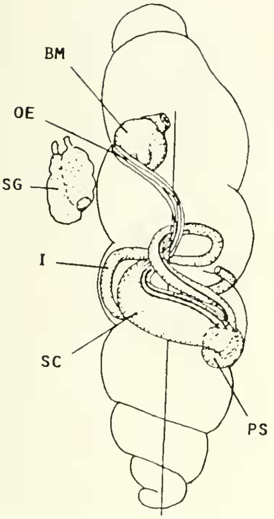


504

FIGS. 505–515: CLAUSILIIDAE
505) *Itala itala*, digestive tract. 4mm.
506) *Itala itala*, morphology of gastric region. 3.4mm.
507) *Itala itala*, kidney internal morphology. 1.9mm.
508) *Itala itala*, pulmonary complex. 5.6mm.
509) *Itala itala*, nervous system in dorsal view. 1.4mm.
510) *Idem*, cerebral commissure cut. 1.4mm.
511) *Albinaria olivieri*, nervous system in dorsal view. 2mm.
512) *Idem*, cerebral commissure cut. 2mm.
513) *Albinaria olivieri*, digestive tract. 4.25mm.
514) *Albinaria olivieri*, pulmonary complex. 8.5mm.
515) *Albinaria olivieri*, kidney internal morphology. 2mm.

505



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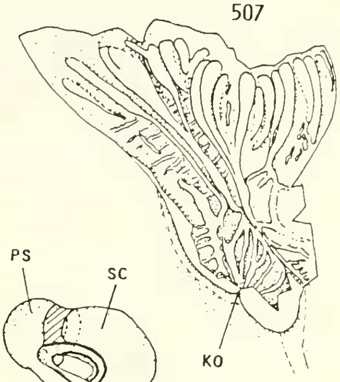

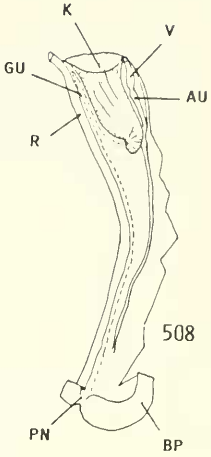

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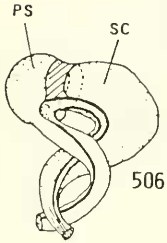

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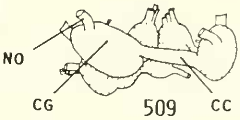

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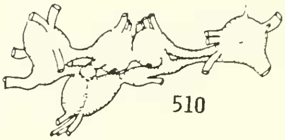

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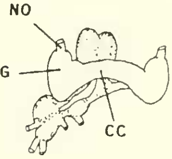

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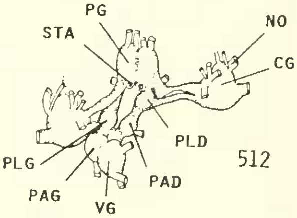

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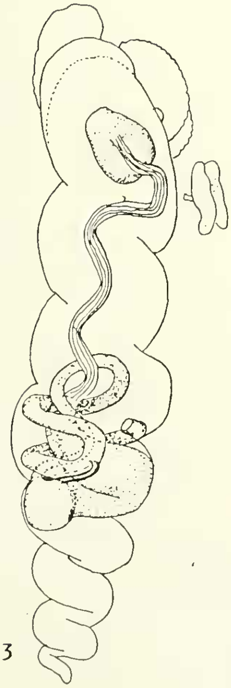

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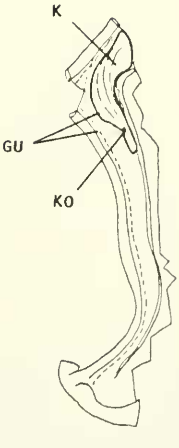

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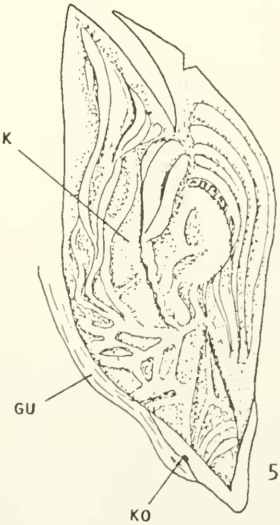
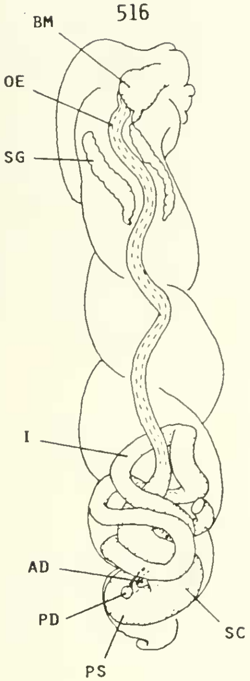


515

FIGS. 516–523: CLAUSILIIDAE, CERIONIDAE
516) *Nenia tridens*, digestive tract. 6mm.
517) *Nenia tridens*, pulmonary complex. 10.6mm.
518) *Nenia tridens*, kidney internal morphology. 3.4mm.
519) *Nenia tridens*, nervous system in dorsal view. 2mm.
520) *Idem*, cerebral commissure cut. 2mm.
521) *Cerion casablancae*, digestive tract. 10mm.
522) *Cerion casablancae*, nervous system in dorsal view. 2mm.
523) *Idem*, cerebral commissure cut. 2mm.

516



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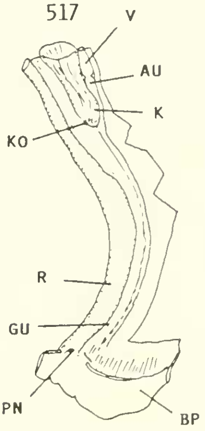

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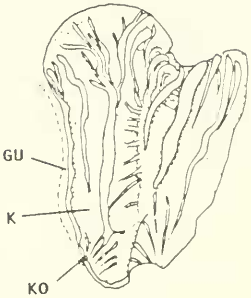

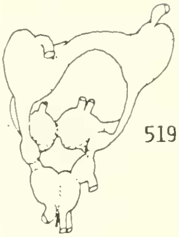

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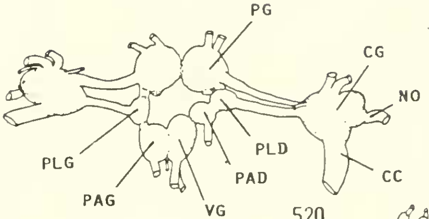

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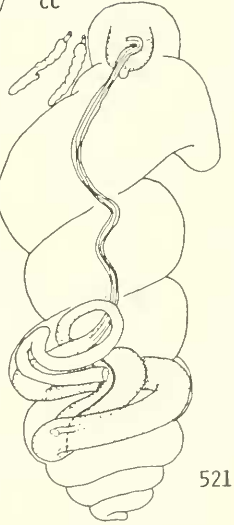

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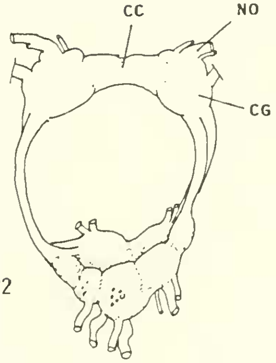

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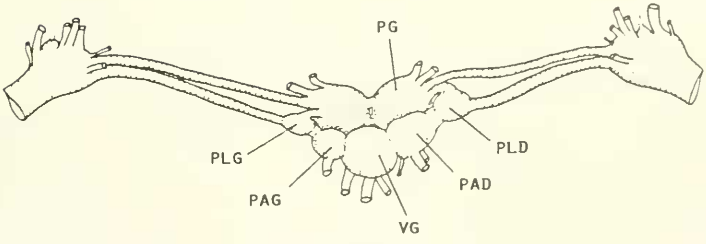
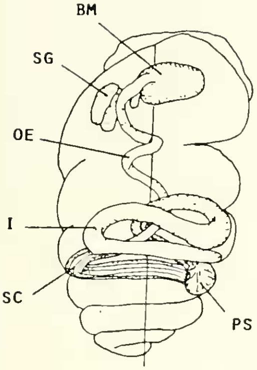


523

FIGS. 524–531: CERIONIDAE, UROCOPTIDAE
524) *Cerion copium,* digestive tract. 10mm.
525) *Cerion copium,* morphology of gastric region. 5mm.
526) *Cerion copium,* kidney internal morphology. 5mm.
527) *Cerion copium,* pulmonary complex. 10mm.
528) *Macroceramus signatus,* pulmonary complex. 5mm.
529) *Macroceramus signatus,* digestive tract. 5mm.
530) *Berendtia taylori,* nervous system in dorsal view. 2.6mm.
531) *Idem,* cerebral commissure cut. 2.6mm.

524



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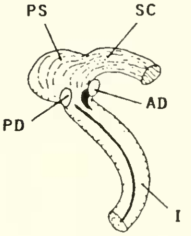

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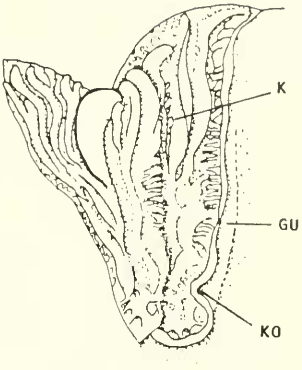

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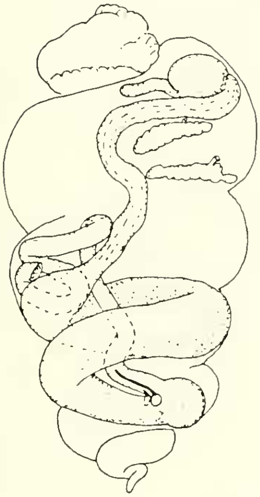

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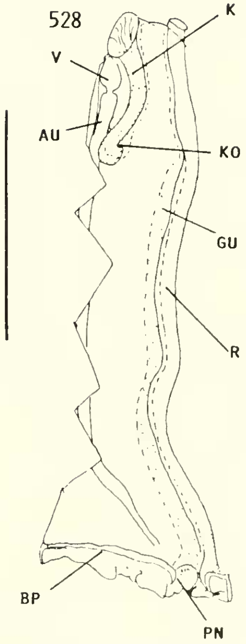

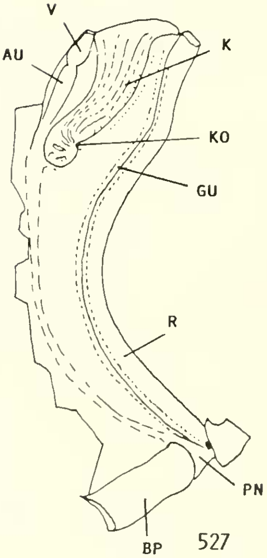

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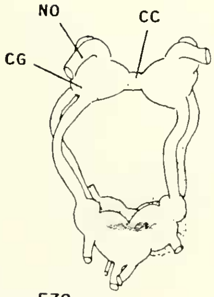

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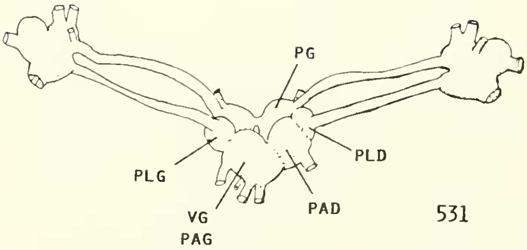
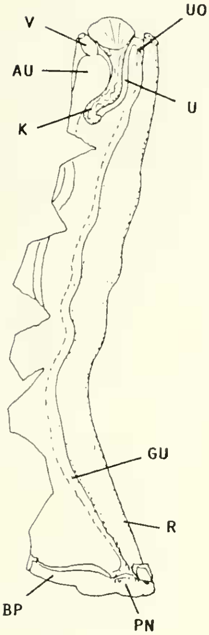


531

FIGS. 532–539: UROCOPTIDAE, BULIMULIDAE (ODONTOSTOMINAE)
532) *Urocoptis procera*, pulmonary complex. 10mm.
533) *Berendtia taylori*, pulmonary complex. 10mm.
534) *Urocoptis procera*, nervous system in dorsal view. 2mm.
535) *Idem*, cerebral commissure cut. 2mm.
536) *Plagiodontes daedaleus*, pulmonary complex. 10.6mm.
537) *Plagiodontes daedaleus*, digestive tract. 9.4mm.
538) *Plagiodontes daedaleus*, nervous system in dorsal view. 2.4mm.
539) *Idem*, cerebral commissure cut. 2.4mm.

532



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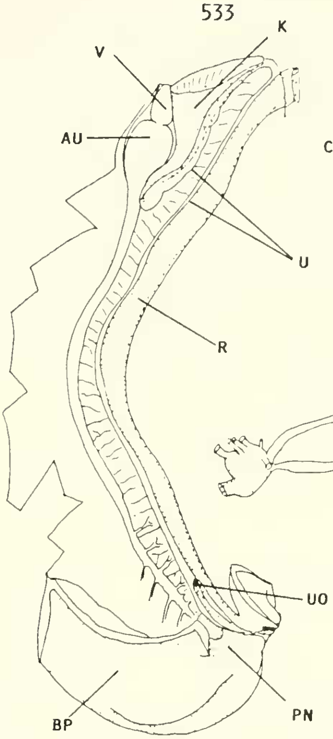

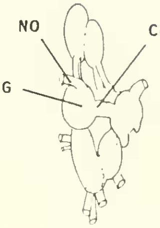

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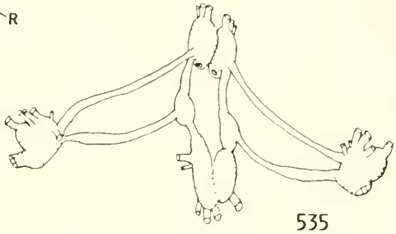

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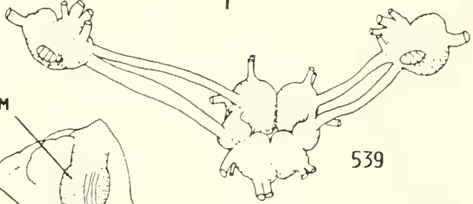

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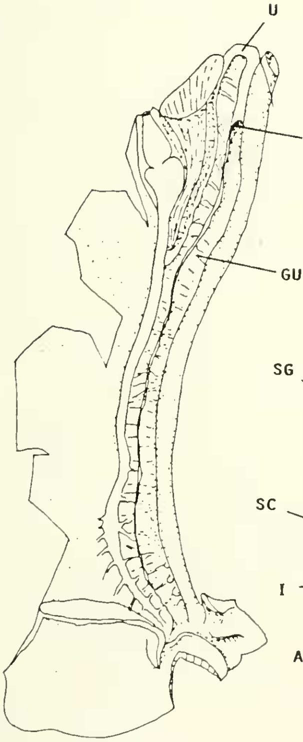

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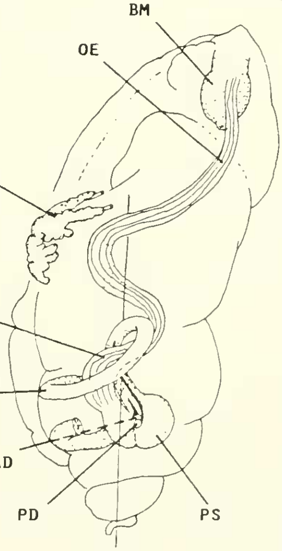

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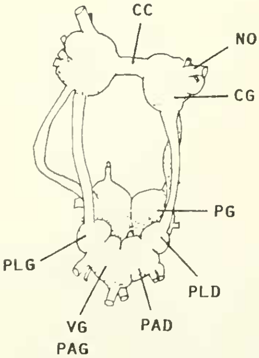
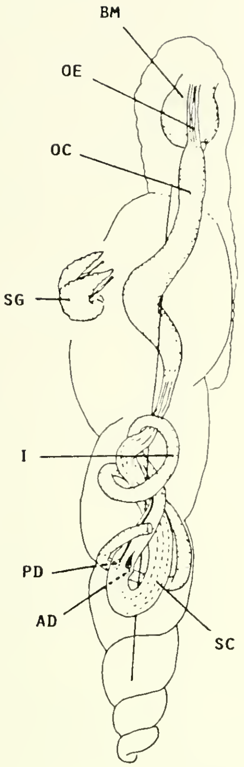


538

FIGS. 540–547: BULIMULIDAE (BULIMULINAE)
540) *Bostryx bermudezae*, digestive tract. 3.7mm.
541) *Bostryx bermudezae*, pulmonary complex. 5mm.
542) *Bostryx bermudezae*, kidney internal morphology. 2mm.
543) *Bostryx bermudezae*, nervous system in dorsal view. 1.5mm.
544) *Idem*, cerebral commissure cut. 1.5mm.
545) *Discoleus azulensis*, digestive tract. 3.9mm.
546) *Discoleus azulensis*, nervous system in dorsal view. 2mm.
547) *Idem*, cerebral commissure cut. 2mm.

540



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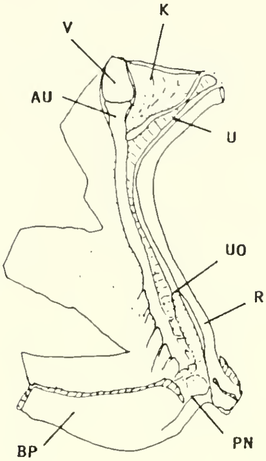

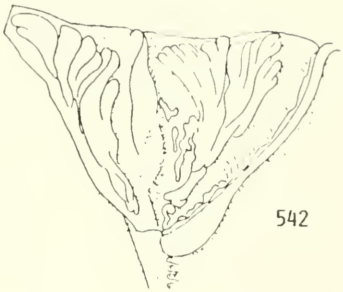

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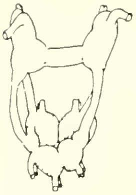

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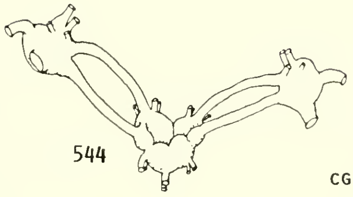

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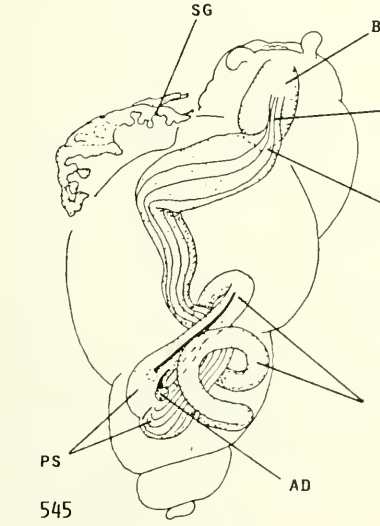

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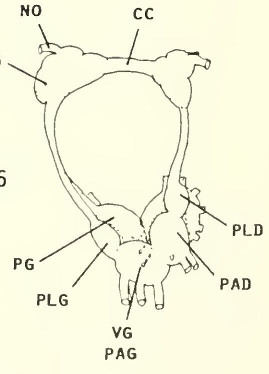

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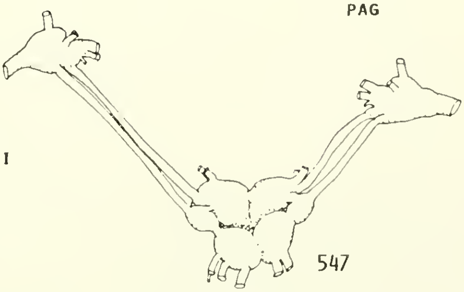

547

FIGS. 548–555: BULIMULIDAE (BULIMULINAE, AMPHIBULIMINAE)
548) *Pellicula depressa*, digestive tract. 0.8mm.
549) *Simpulopsis miersi*, nervous system in dorsal view. 2.5mm.
550) *Idem*, cerebral commissure cut. 2.5mm.
551) *Pellicula depressa*, nervous system in dorsal view. 2.5mm.
552) *Idem*, cerebral commissure cut. 2.5mm.
553) *Simpulopsis miersi*, pulmonary complex. 8.4mm.
554) *Simpulopsis miersi*, kidney internal morphology. 4.5mm.
555) *Simpulopsis miersi*, digestive tract. 5.8mm.

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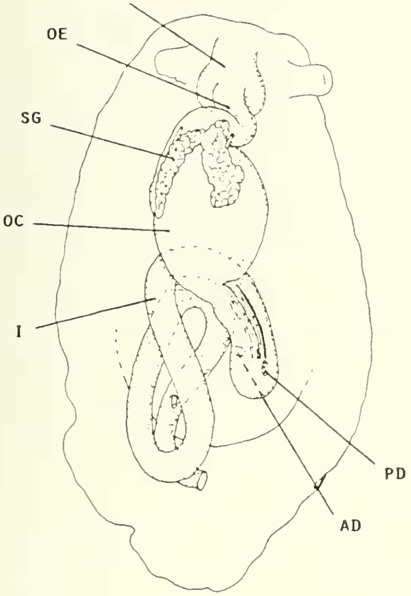

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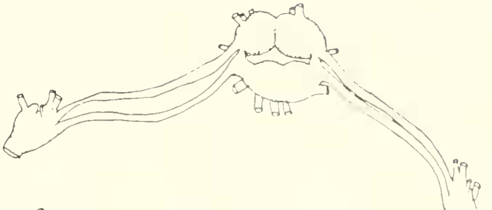

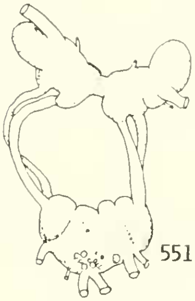

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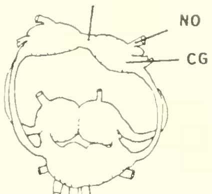

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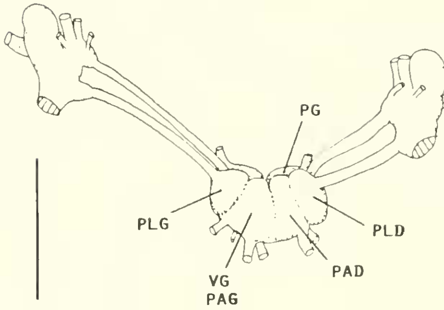

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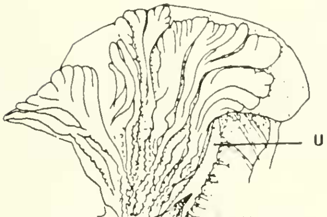

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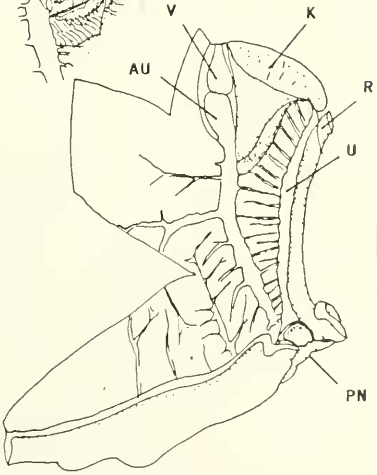

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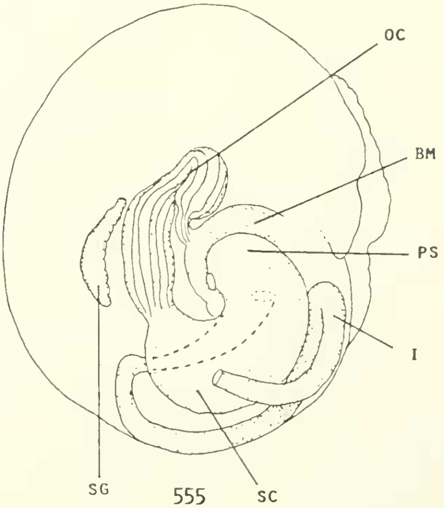
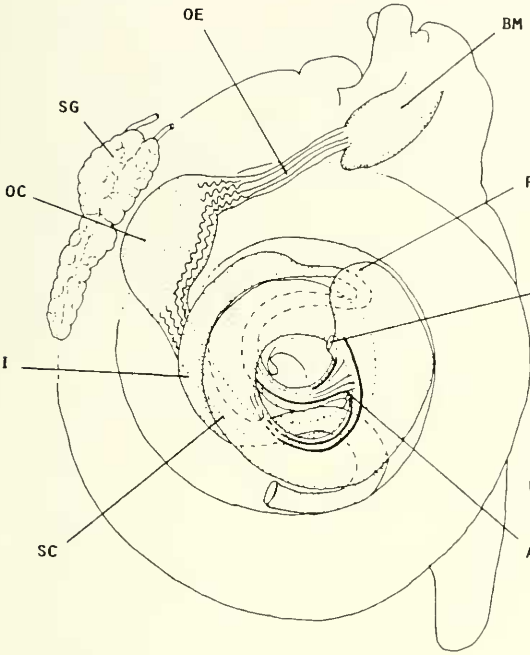


555

FIGS. 556–561: CAMAENIDAE (?)
556) *Solaropsis undata*, digestive tract. 11mm.
557) *Labyrinthus leprieurii*, nervous system in dorsal view. 2mm.
558) *Idem*, cerebral commissure cut. 2mm.
559) *Labyrinthus leprieurii*, digestive tract. 5.9mm.
560) *Labyrinthus leprieurii*, pulmonary complex. 13mm.
561) *Labyrinthus leprieurii*, kidney internal morphology. 3.7mm.

556



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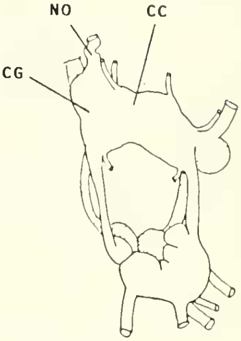

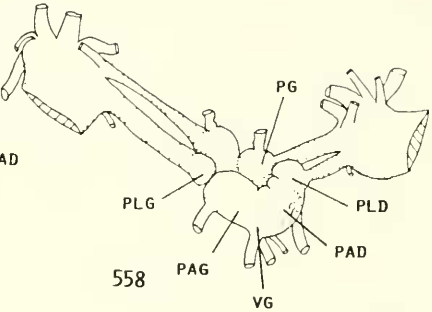

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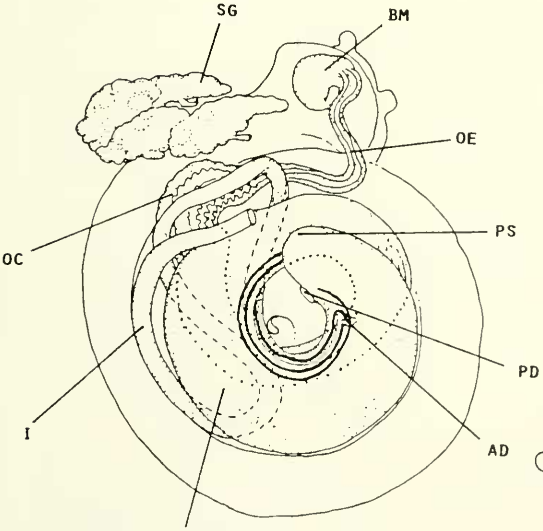

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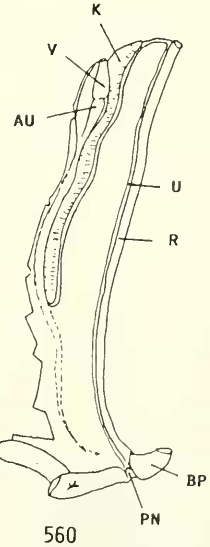

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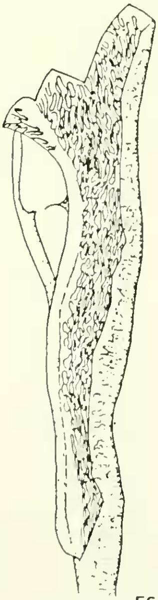

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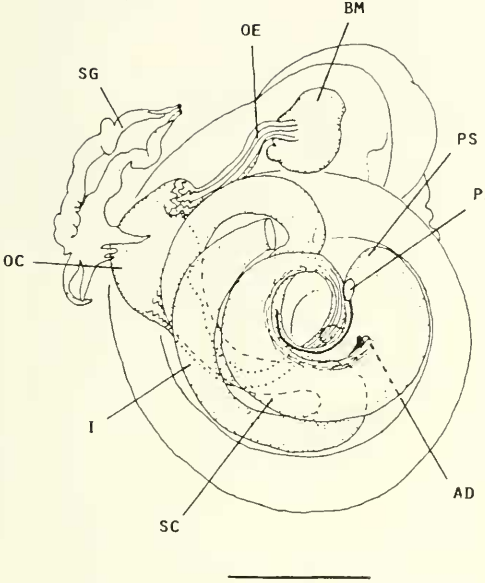
FIGS. 562–568: CAMAENIDAE (?)
562) *Pleurodonte lychnuchus*, digestive tract. 8.4mm.
563) *Pleurodonte lychnuchus*, pulmonary complex. 13.5mm.
564) *Pleurodonte lychnuchus*, kidney internal morphology. 4.5mm.
565) *Amphidromus cognatus*, digestive tract. 10mm.
566) *Pleurodonte lychnuchus*, cerebral ganglia in dorsal view, sheath dissected. 2.5mm.
567) *Pleurodonte lychnuchus*, nervous system in dorsal view. 2.5mm.
568) *Idem*, cerebral commissure cut. 2.5mm.

562



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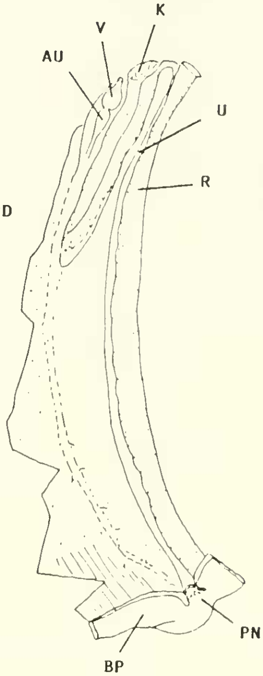

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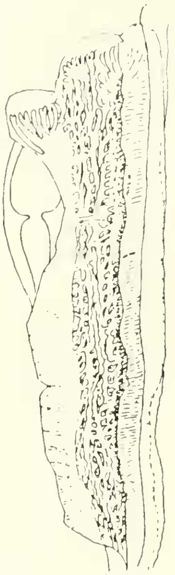

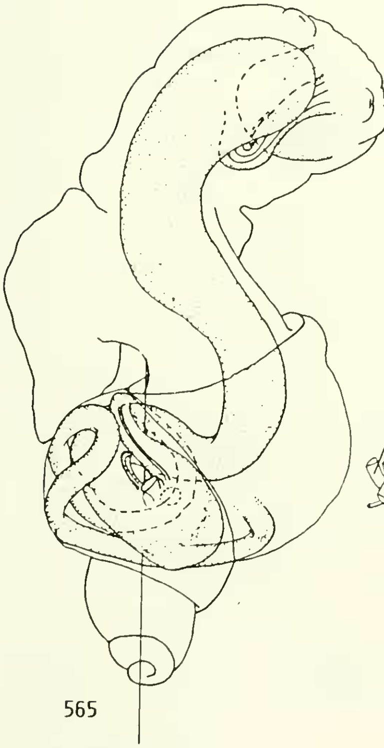

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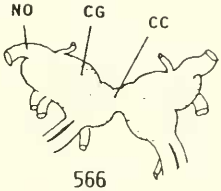

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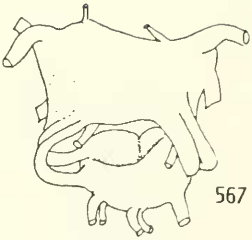

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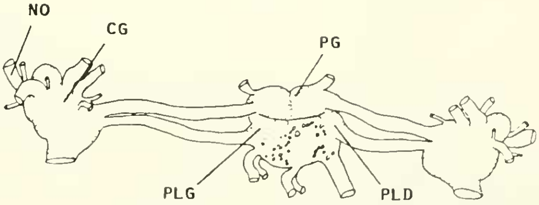
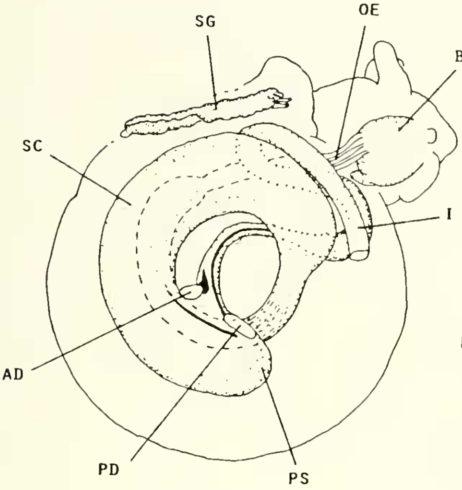


568

FIGS. 569–576: CAMAENIDAE
569) *Plectotropis goniocheila,* digestive tract. 5mm.
570) *Plectotropis goniocheila,* nervous system in dorsal view. 1.6mm.
571) *Idem,* cerebral commissure cut. 1.8mm.
572) *Amplirhagada burnerensis,* nervous system in dorsal view. 4mm.
573) *Idem,* cerebral commissure cut. 4mm.
574) *Amplirhagada burnerensis,* digestive tract. 10mm.
575) *Amplirhagada burnerensis,* pulmonary complex. 20mm.
576) *Amplirhagada burnerensis,* kidney internal morphology. 6mm.

569



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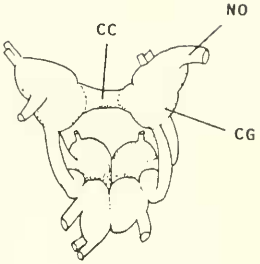

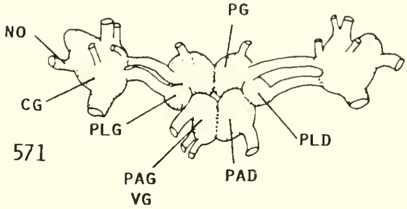

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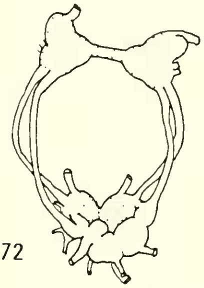

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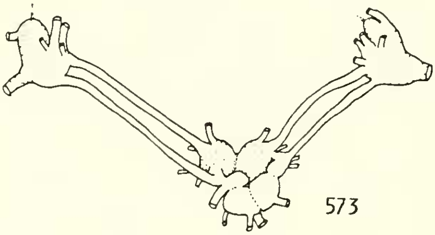

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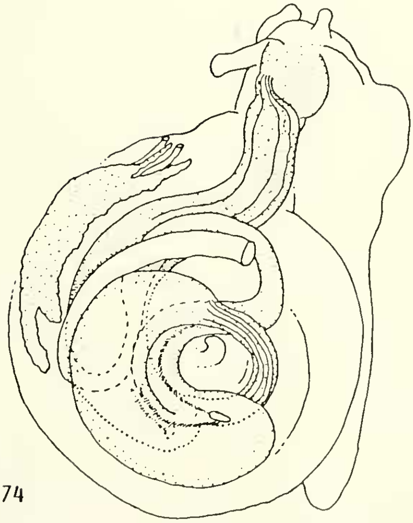

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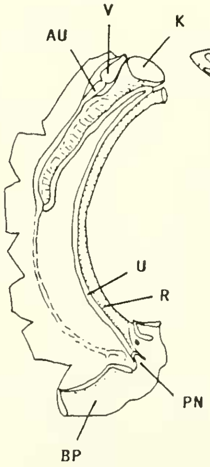

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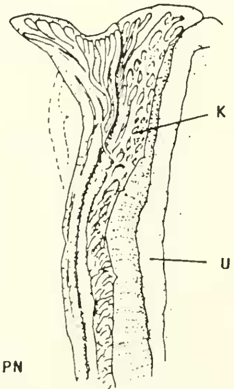

576

FIGS. 577–583: POLYGYRIDAE (POLYGYRINAE)
577) *Polygyra matermontana*, digestive tract. 4.4mm.
578) *Polygyra matermontana*, kidney internal morphology. 3.6mm.
579) *Polygyra matermontana*, pulmonary complex. 5.4mm.
580) *Trilobopsis trachypepla*, digestive tract. 1.2mm.
581) *Mesodon andrewsae*, digestive tract. 10.6mm.
582) *Polygyra matermontana*, nervous system in dorsal view. 2mm.
583) *Idem*, cerebral commissure cut. 2mm.

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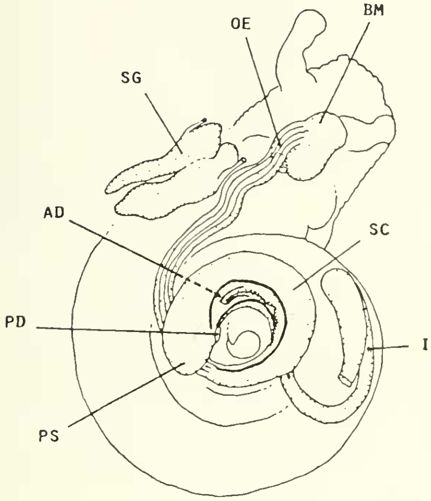

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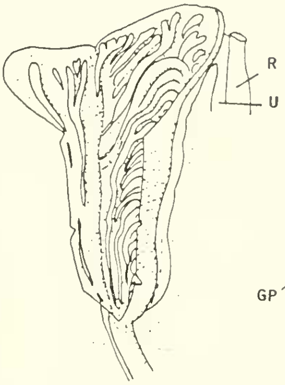

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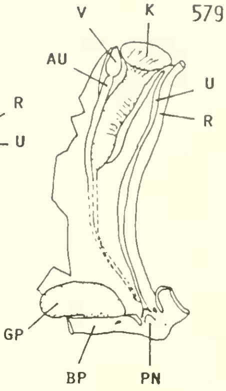

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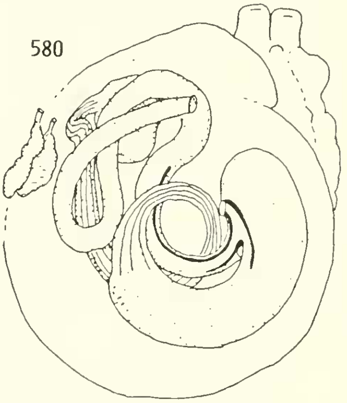

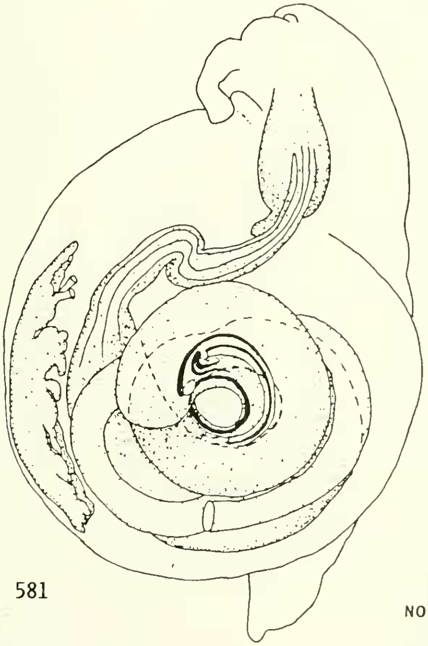

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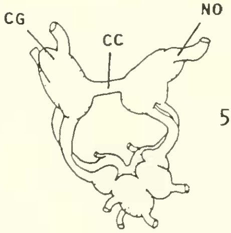

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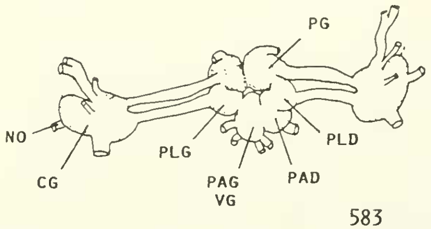
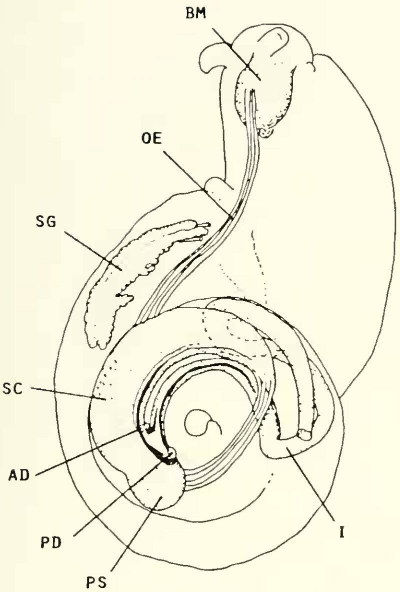


583

FIGS. 584–591: POLYGYRIDAE (TRIODOPSINAE), BRADYBAENIDAE
584) *Triodopsis fraudulenta*, digestive tract. 8mm.
585) *Triodopsis fraudulenta*, nervous system in dorsal view. 2mm.
586) *Idem*, cerebral commissure cut. 2mm.
587) *Bradybaena tourannensis*, digestive tract. 6.8mm.
588) *Bradybaena tourannensis*, pulmonary complex. 6mm.
589) *Bradybaena tourannensis*, kidney internal morphology. 10.6mm.
590) *Bradybaena tourannensis*, nervous system in dorsal view. 2mm.
591) *Idem*, cerebral commissure cut. 2mm.

584



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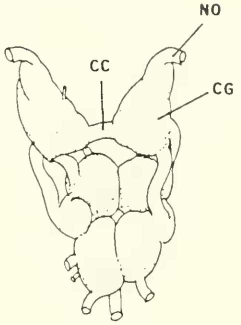

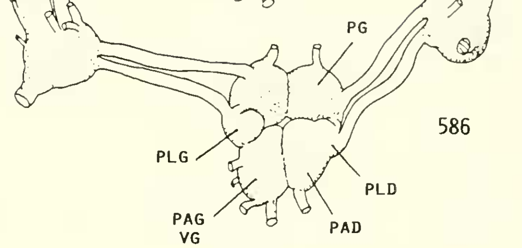

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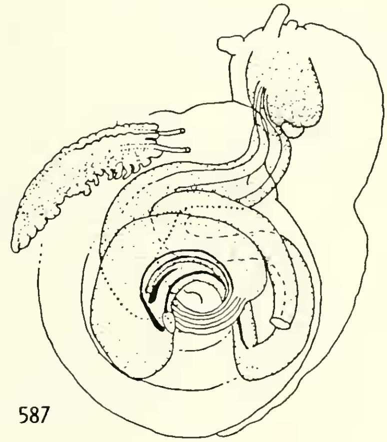

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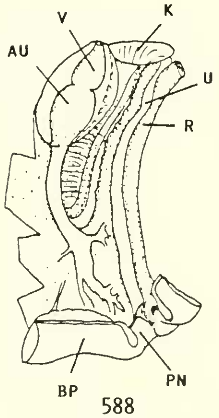

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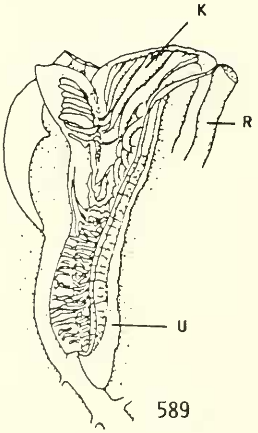

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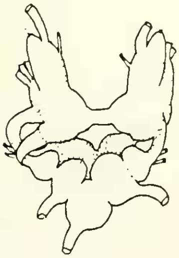

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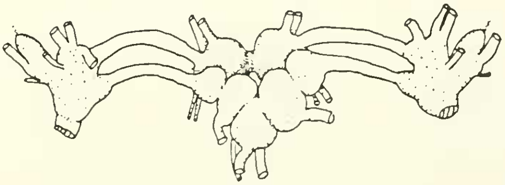
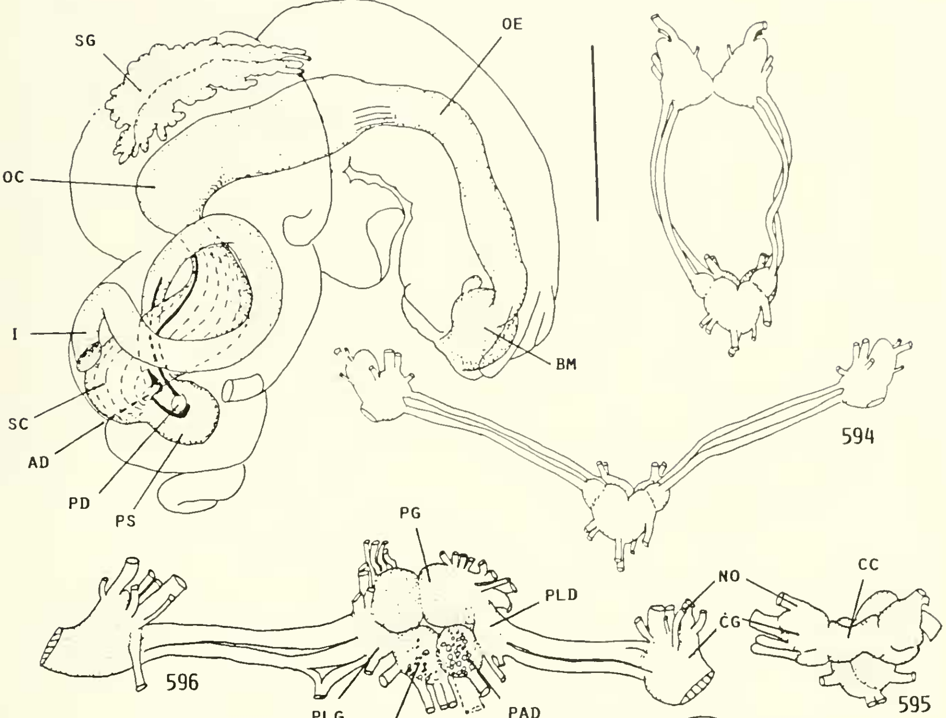


591

FIGURES 592–599: BRADYBAENIDAE, HAPLOTREMATIDAE
592) *Helicostylus palawanensis*, digestive tract. 13mm.
593) *Helicostylus palawanensis*, nervous system in dorsal view. 5mm.
594) *Idem*, cerebral commissure cut. 5mm.
595) *Haplotrema minimum*, nervous system in dorsal view. 1.8mm.
596) *Idem*, cerebral commissure cut. 1.8mm.
597) *Haplotrema concavum*, digestive tract. 6.3mm.
598) *Haplotrema concavum*, pulmonary complex. 13mm.
599) *Haplotrema concavum*, kidney internal morphology. 6.3mm.



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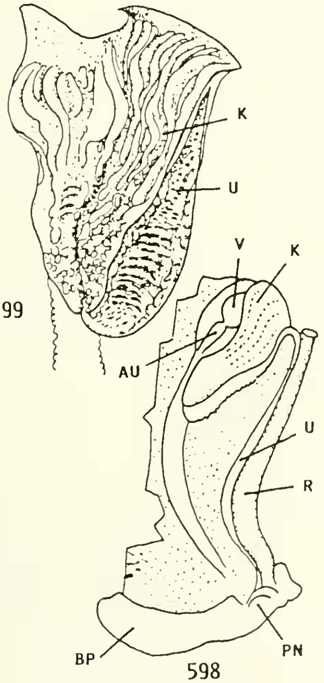

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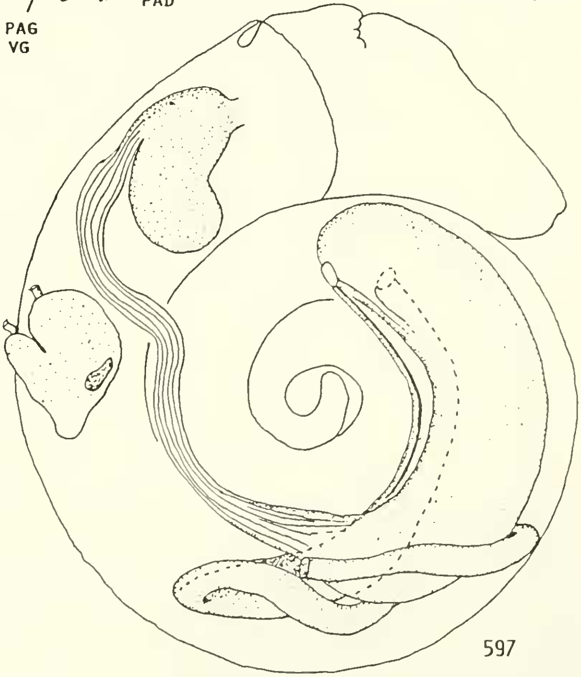
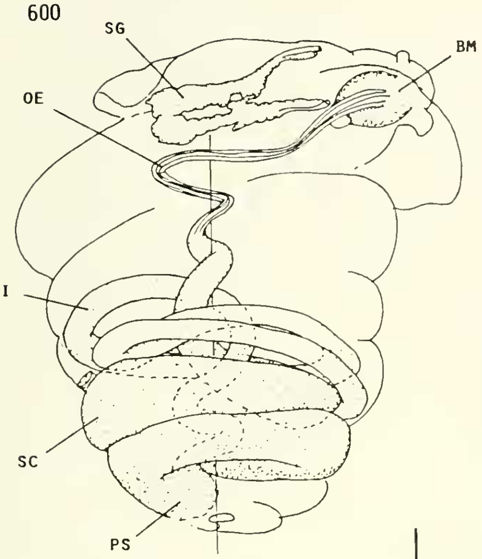
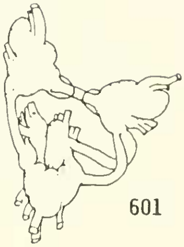


597

FIGS. 600–606: SAGDIDAE
600) *Sagda grandis*, digestive tract. 6.7mm.
601) *Sagda grandis*, nervous system in dorsal view. 2.5mm.
602) *Idem*, cerebral commissure cut. 2.5mm.
603) *Proserpinula opalina*, nervous system in dorsal view. 2mm.
604) *Idem*, cerebral commissure cut. 2mm.
605) *Proserpinula opalina*, pulmonary complex. 2.7mm.
606) *Proserpinula opalina*, digestive tract. 2.5mm.

600





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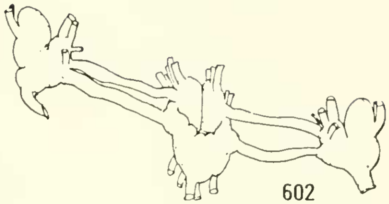

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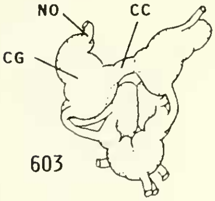

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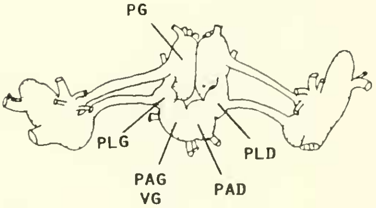

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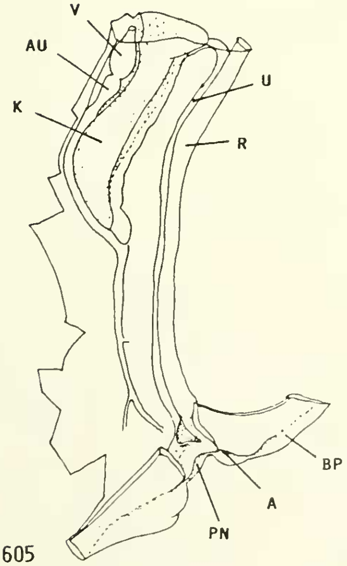

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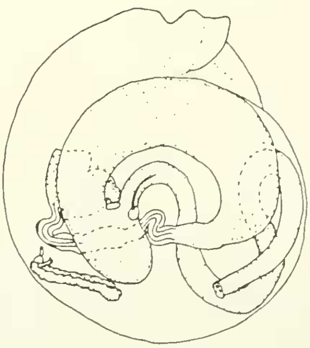
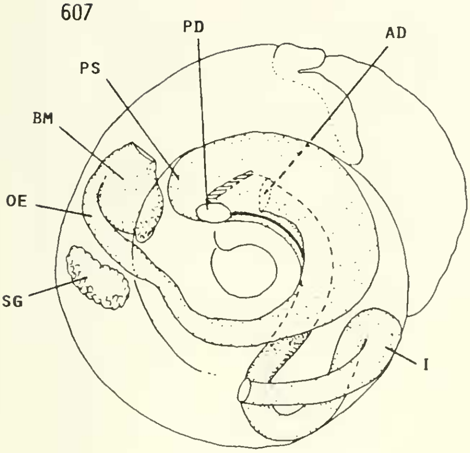
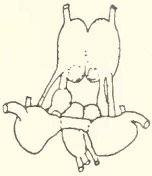


606

FIGS. 607–614: HELMINTHOGLYPTIDAE (THYSANOPHORINAE, CEPOLINAE)
607) *Thysanophora horni,* digestive tract. 1.5mm.
608) *Thysanophora horni,* nervous system in dorsal view. 1mm.
609) *Idem,* cerebral commissure cut. 1mm.
610) *Thysanophora horni,* pulmonary complex. 0.9mm.
611) *Thysanophora horni,* kidney internal morphology. 2.2mm.
612) *Cepolis varians,* nervous system in dorsal view. 6.8mm.
613) *Idem,* cerebral commissure cut. 2.8mm.
614) *Cepolis varians,* digestive tract. 2.8mm.

607





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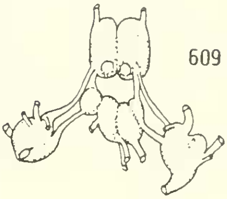

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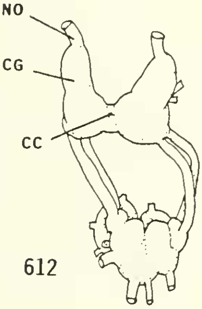

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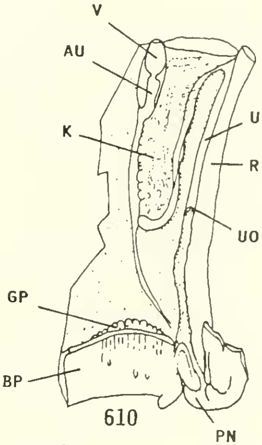

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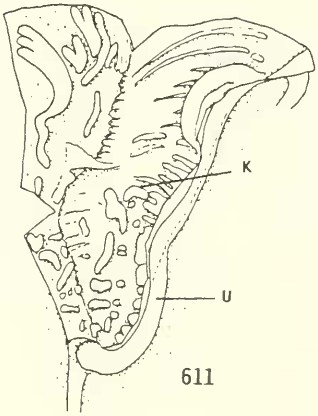

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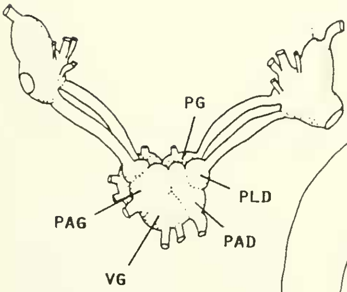

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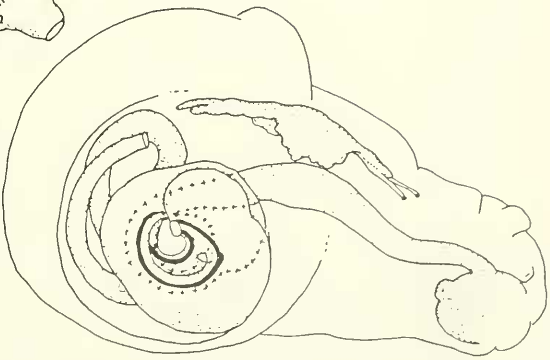
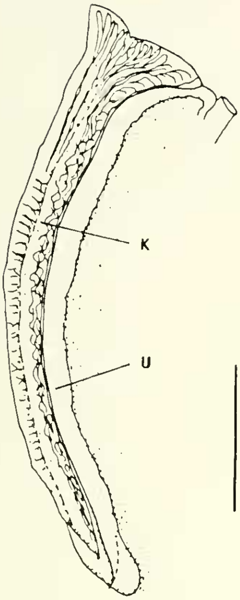


614

FIGS. 615–622: HELMINTHOGLYPTIDAE (CEPOLINAE)
615) *Cepolis varians*, kidney internal morphology. 5mm.
616) *Cepolis varians*, pulmonary complex. 8.75mm.
617) *Psadara nubeculata*, kidney internal morphology. 4.2mm.
618) *Psadara nubeculata*, pulmonary complex. 7.7mm.
619) *Psadara nubeculata*, nervous system in dorsal view. 1.6mm.
620) *Idem*, cerebral commissure cut. 1.6mm.
621) *Cepolis maynardi*, digestive tract. 5mm.
622) *Psadara marmatensis*, digestive tract. 3.3mm.

615



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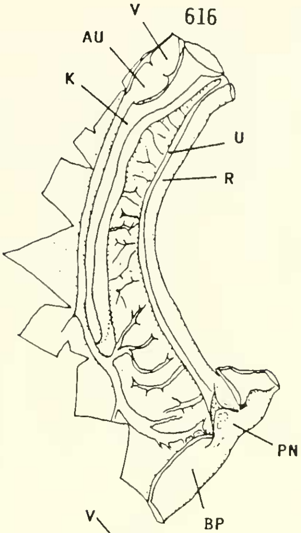

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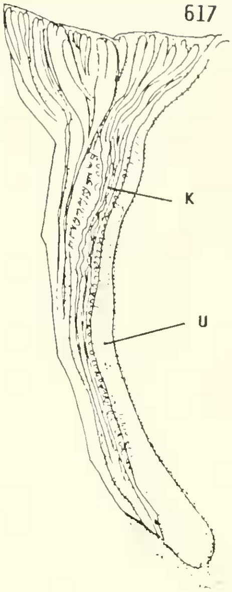

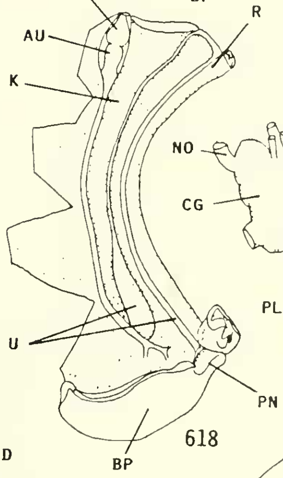

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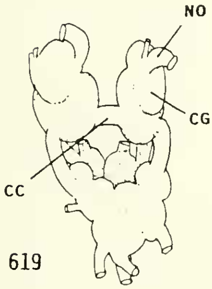

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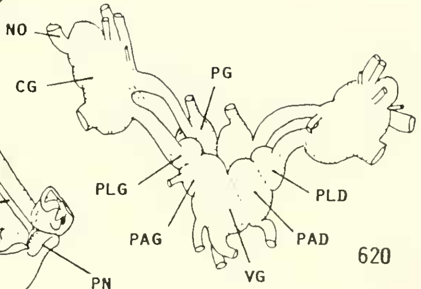

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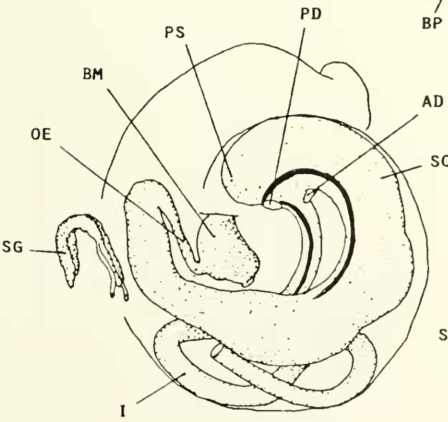

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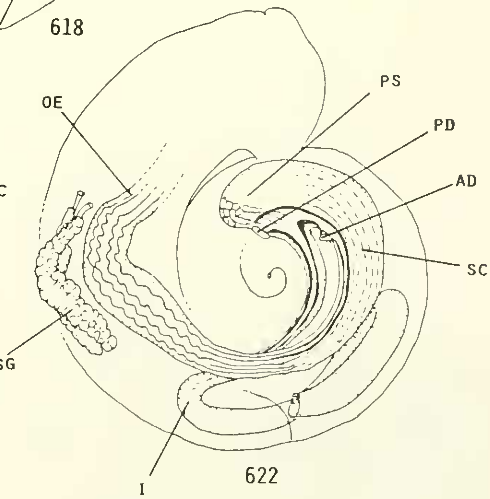
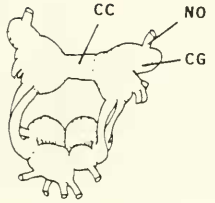


622

FIGS. 623–629: HELMINTHOGLYPTIDAE (XANTHONYCINAE, SONORELLINAE)
623) *Averellia coactiliata*, digestive tract. 3.9mm.
624) *Averellia coactiliata*, nervous system in dorsal view. 2mm.
625) *Idem*, cerebral commissure cut. 2mm.
626) *Sonorella walkeri*, nervous system in dorsal view. 2mm.
627) *Idem*, cerebral commissure cut. 2mm.
628) *Sonorella walkeri*, pulmonary complex. 8.5mm.
629) *Sonorella walkeri*, digestive tract. 8.5mm.

624



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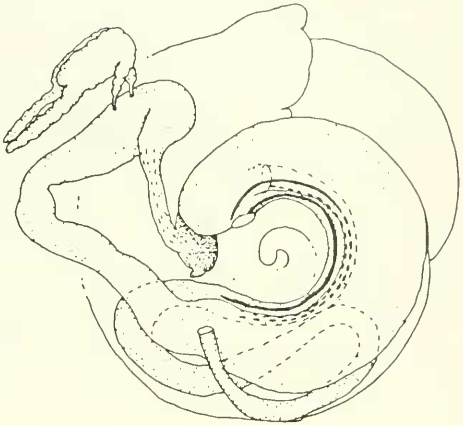

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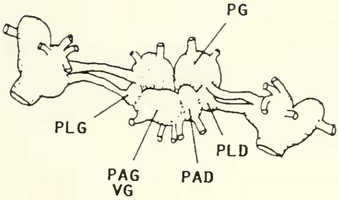

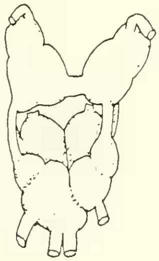

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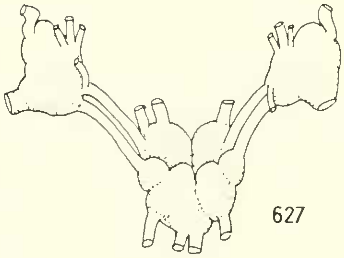

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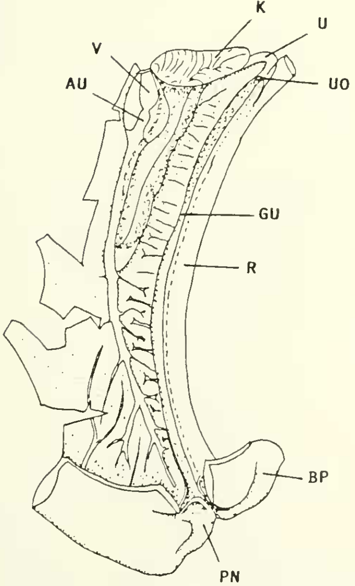

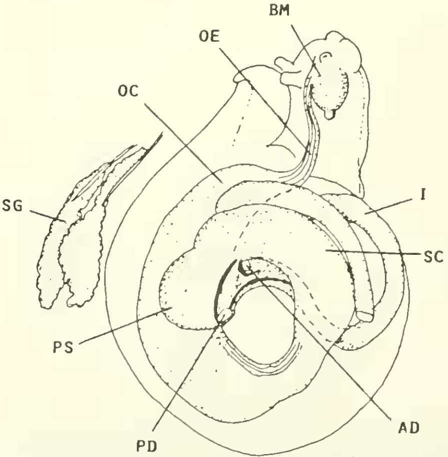

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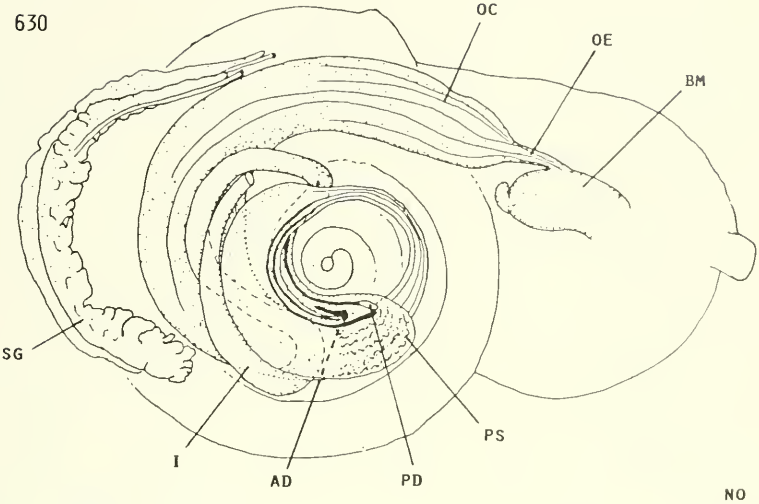
629

FIGS. 630–634: HELMINTHOGLYPTIDAE (HELMINTHOGLYPTINAE)
630) *Helminthoglypta sequoicola*, digestive tract. 10mm.
631) *Helminthoglypta sequoicola*, nervous system in dorsal view. 4.4mm.
632) *Idem*, cerebral commissure cut. 4.4mm.
633) *Helminthoglypta sequoicola*, kidney internal morphology. 10mm.
634) *Helminthoglypta sequoicola*, pulmonary complex. 16mm.

630



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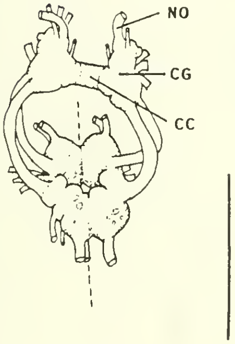

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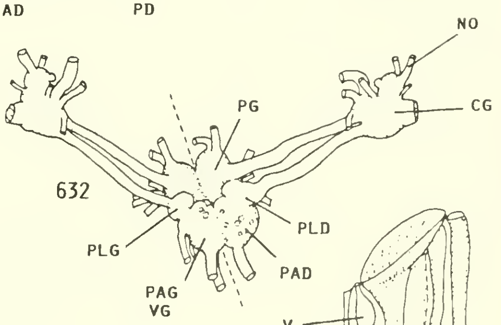

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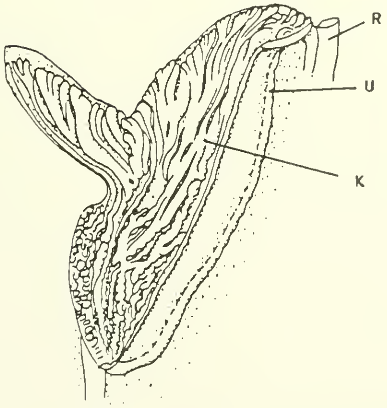

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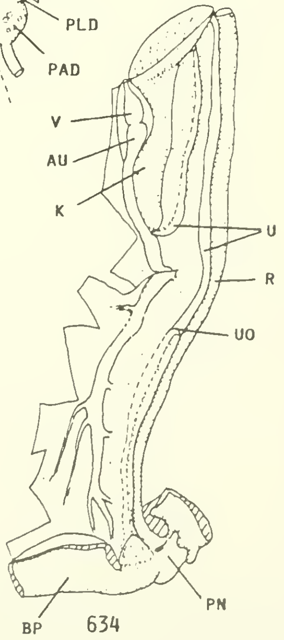
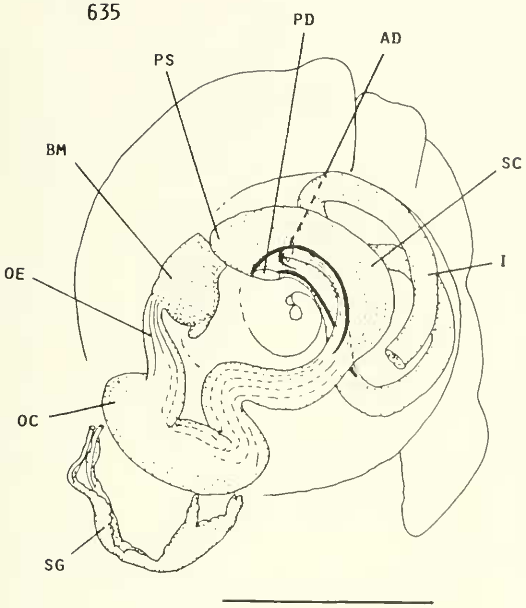


FIGS. 635–639: HELMINTHOGLYPTIDAE (HELMINTHOGLYPTINAE)
635) *Epiphragmopora claromphalos*, digestive tract. 10mm.
636) *Epiphragmopora claromphalos*, pulmonary complex. 1.7mm.
637) *Epiphragmopora claromphalos*, nervous system in dorsal view. 4.7mm.
638) *Idem*, cerebral commissure cut. 4.7mm.
639) *Monadenia fidelis*, digestive tract. 12.5mm.

635



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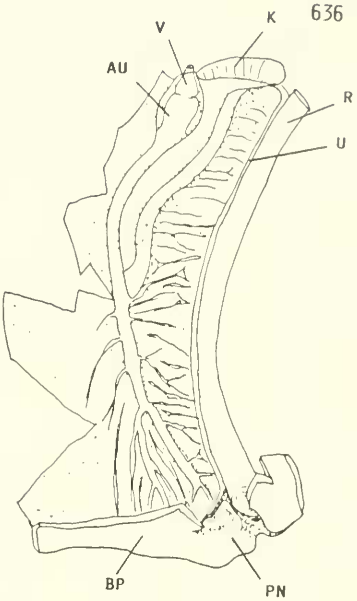

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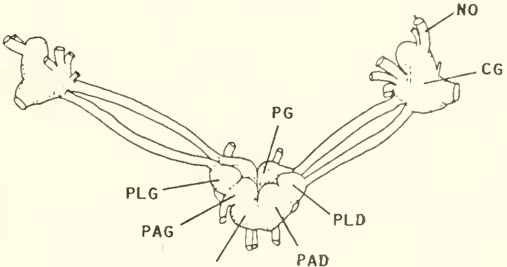

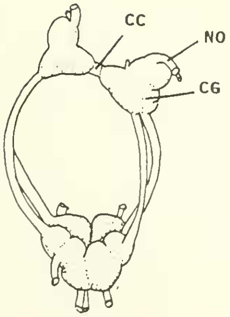

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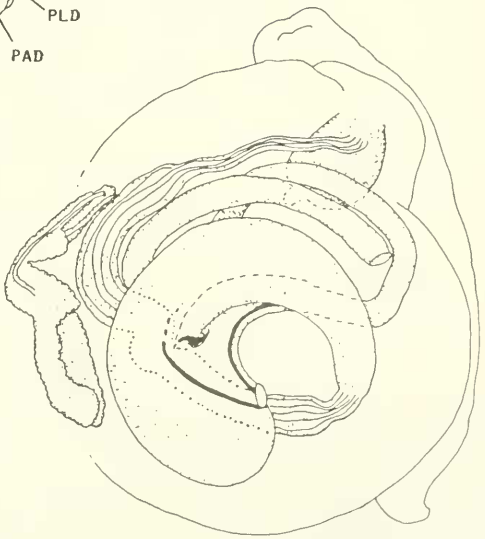
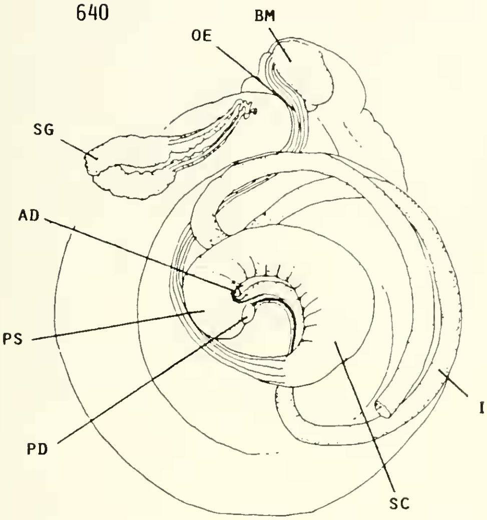


639

FIGS. 640–647: HELICIDAE (SPHINCTEROCHILINAE)
640) *Sphincterochila zonata,* digestive tract. 6.1mm.
641) *Sphincterochila zonata,* pulmonary complex. 10.3mm.
642) *Sphincterochila zonata,* kidney internal morphology. 5.9mm.
643) *Sphincterochila zonata,* nervous system in dorsal view, cerebral commissure cut. 2.5mm.
644) *Sphincterochila zonata,* nervous system in dorsal view. 2.5mm.
645) *Halolimnohelix sericata,* nervous system in dorsal view. 2mm.
646) *Idem,* cerebral commissure cut. 2mm.
647) *Halolimnohelix sericata,* digestive tract. 7.8mm.

640



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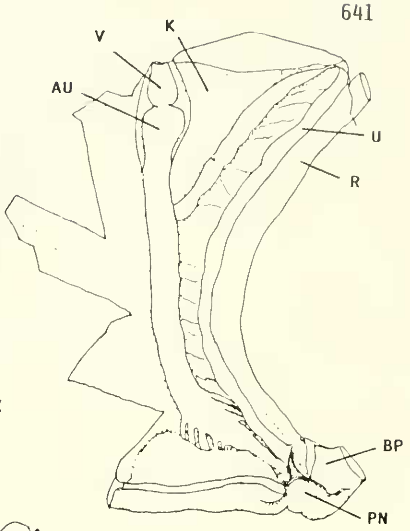

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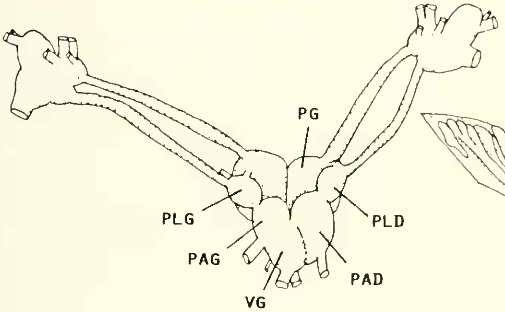

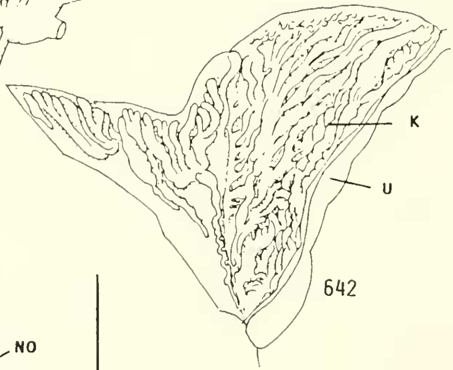

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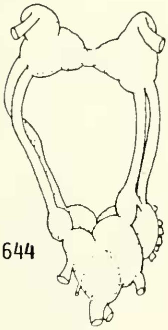

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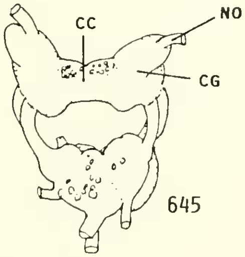

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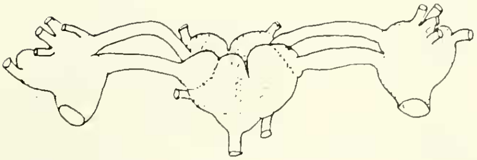

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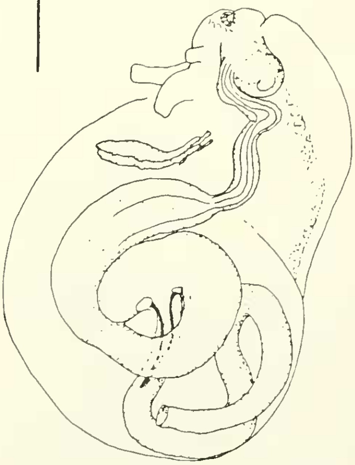

647

FIGS. 648–657: HELICIDAE (SPHINCTEROCHILINAE, HELICODONTINAE)
648) *Halolimnohelix sericata*, pulmonary complex. 10mm.
649) *Halolimnohelix sericata*, kidney internal morphology. 7.4mm.
650) *Cochlicella acuta*, digestive tract. 6.25mm.
651) *Cochlicella acuta*, nervous system in dorsal view. 2mm.
652) *Idem*, cerebral commissure cut. 2mm.
653) *Helicodonta obvoluta*, nervous system in dorsal view. 2.3mm.
654) *Idem*, cerebral commissure cut. 2.3mm.
655) *Cochlicella acuta*, pulmonary complex. 5.7mm.
656) *Helicodonta obvoluta*, pulmonary complex. 6.6mm.
657) *Helicodonta obvoluta*, digestive tract. 8mm.

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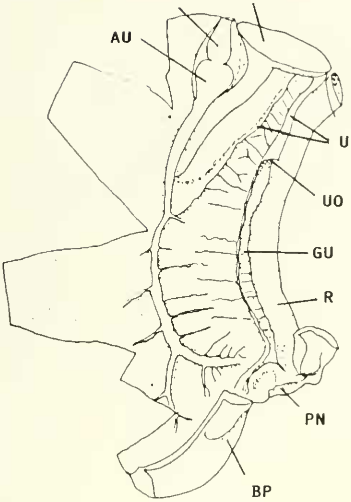

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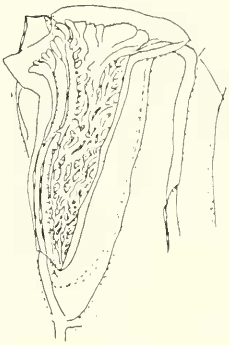

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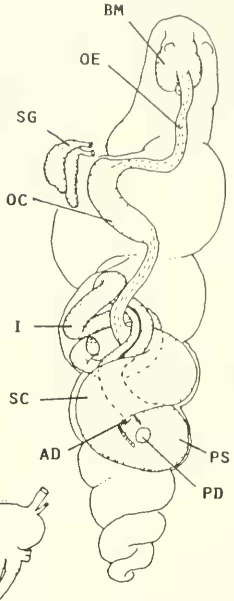

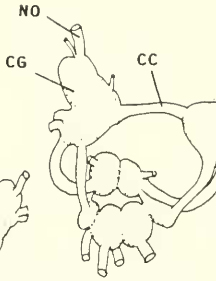

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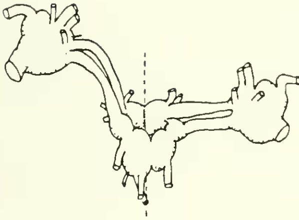

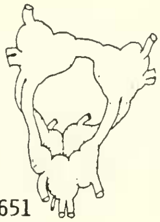

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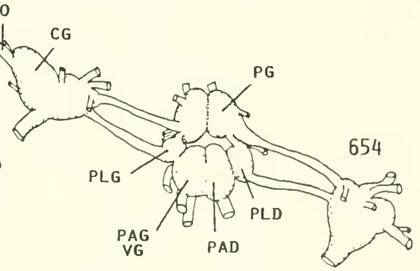

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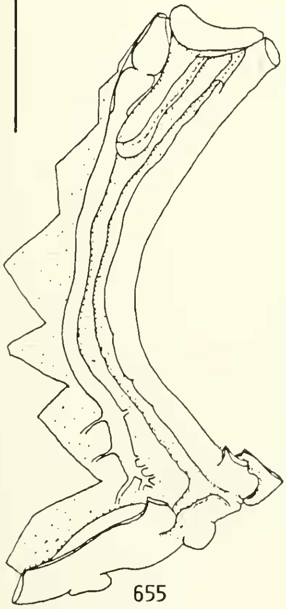

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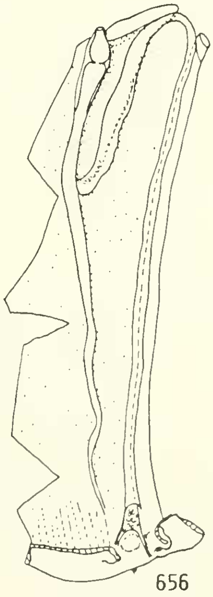

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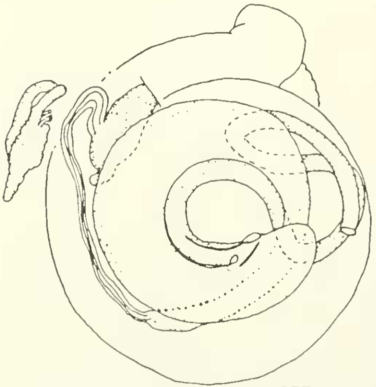
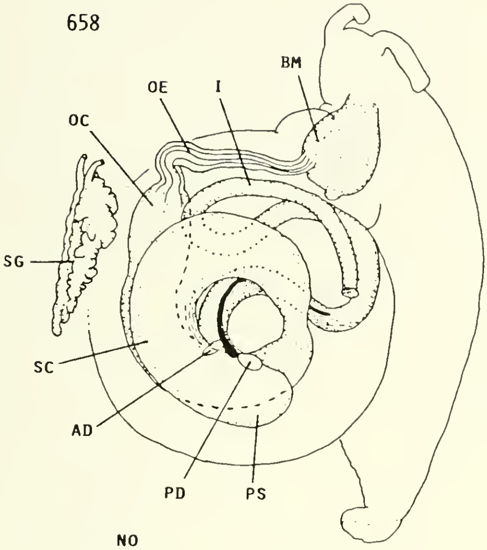


657

FIGS. 658–664: HELICIDAE (HYGROMIINAE)
658) *Hygromia limbata*, digestive tract. 7mm.
659) *Trichia hispida*, nervous system in dorsal view. 2mm.
660) *Idem,* cerebral commissure cut. 2mm.
661) *Hygromia limbata*, nervous system in dorsal view. 2mm.
662) *Idem,* cerebral commissure cut. 2mm.
663) *Trichia hispida*, pulmonary complex. 6.3mm.
664) *Trichia hispida*, kidney internal morphology. 3.1mm.

658



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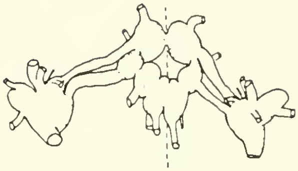

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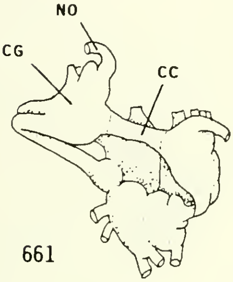

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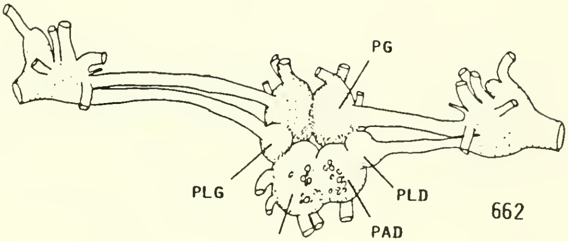

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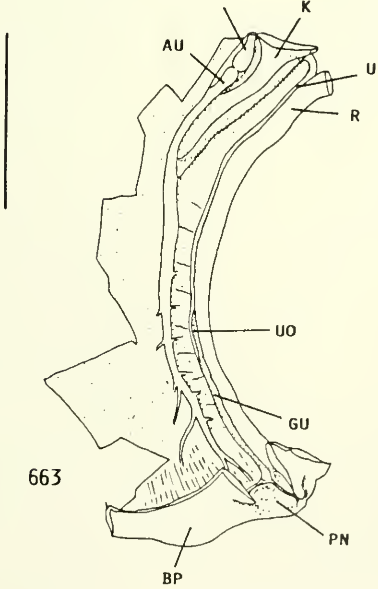

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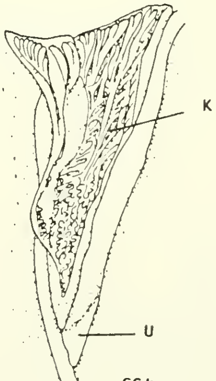
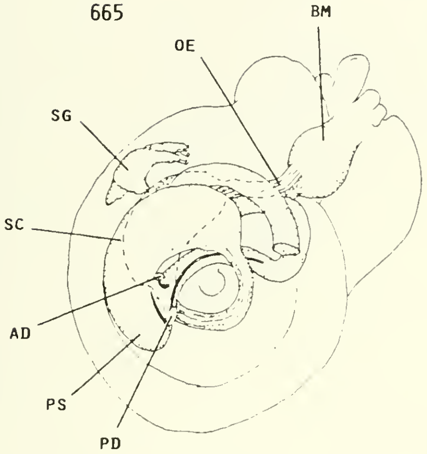


664

FIGS. 665–671: HELICIDAE (HYGROMIINAE)
665) *Helicopsis striata,* digestive tract. 4.4mm.
666) *Helicopsis striata,* pulmonary complex. 4.8mm.
667) *Helicopsis* sp., pulmonary complex. 1mm.
668) *Helicopsis* sp., kidney internal morphology. 1mm.
669) *Helicopsis* sp., nervous system in dorsal view. 1.4mm.
670) *Idem,* cerebral commissure cut. 1.4mm.
671) *Helicopsis* sp., digestive tract. 2.2mm.

665



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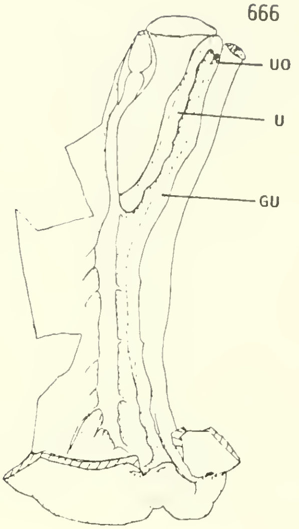

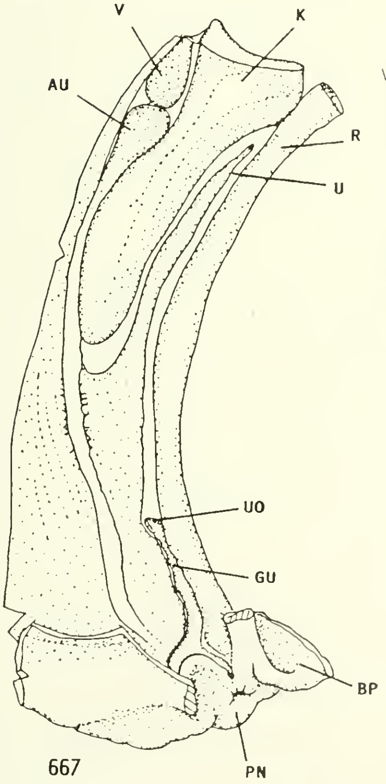

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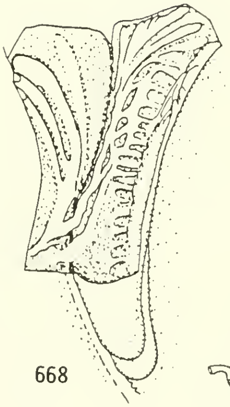

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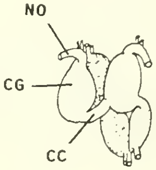

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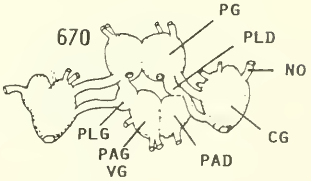
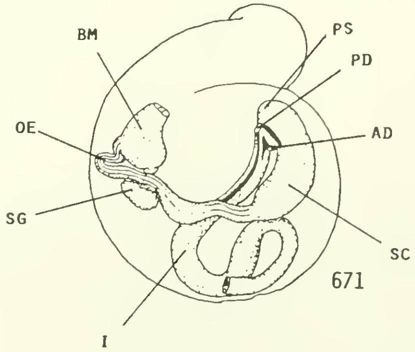
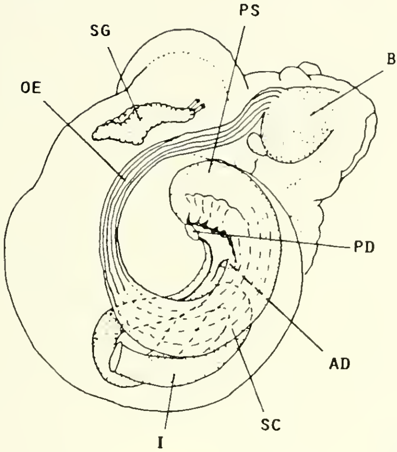




671

FIGS. 672–679: HELICIDAE (HYGROMIINAE, HELICELLINAE)
672) *Candidula unifasciata*, digestive tract. 3.5mm.
673) *Candidula unifasciata*, pulmonary complex. 1.8mm.
674) *Candidula unifasciata*, nervous system in dorsal view. 1.7mm.
675) *Idem*, cerebral commissure cut. 1.7mm.
676) *Monacha cartusiana*, nervous system in dorsal view. 2mm.
677) *Idem*, cerebral commissure cut. 2mm.
678) *Monacha cartusiana*, digestive tract. 6.25mm.
679) *Monacha cartusiana*, pulmonary complex. 6.8mm.

672



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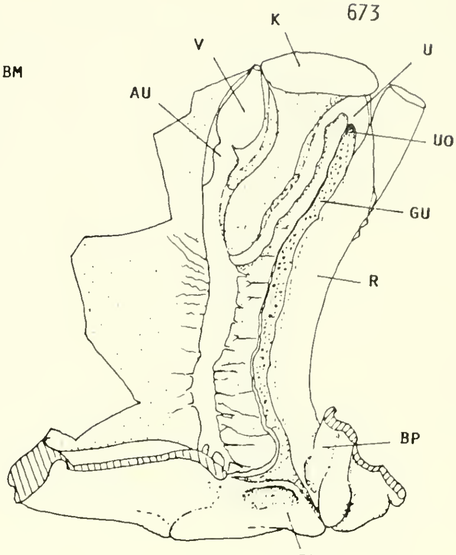

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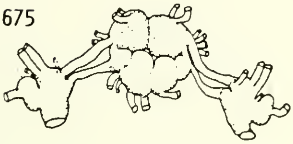

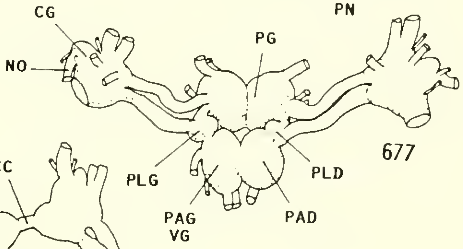

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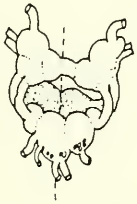

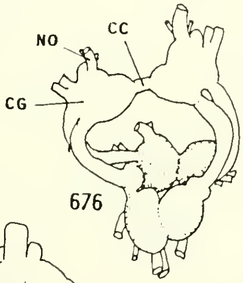

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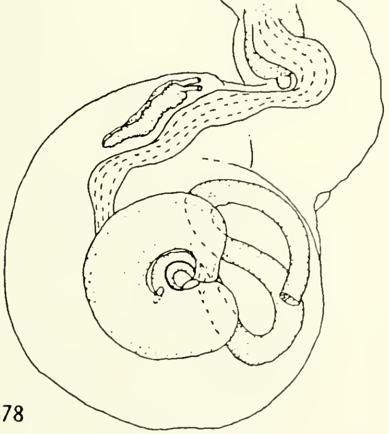

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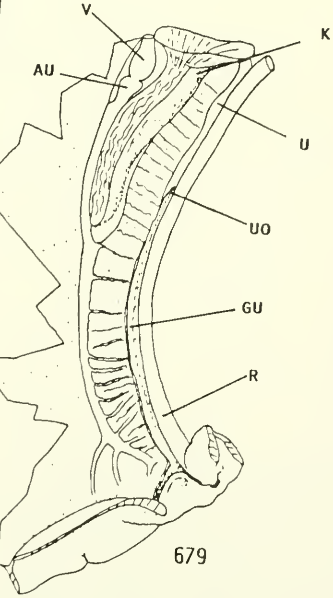

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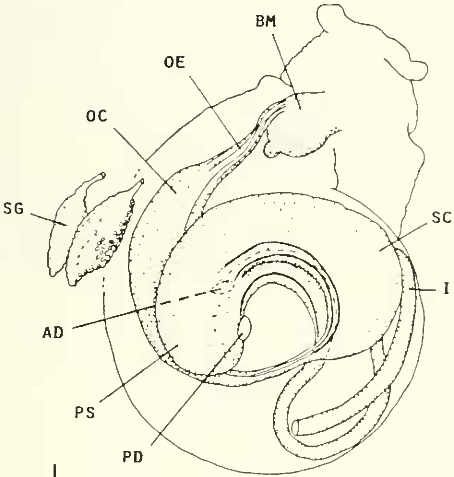
FIGS. 680–686: HELICIDAE (HELICELLINAE, CAMPYLEINAE)
680) *Helicella itala,* digestive tract. 6mm.
681) *Leucochroa explanata,* pulmonary complex. 5mm.
682) *Helicella itala,* nervous system in dorsal view. 2mm.
683) *Idem,* cerebral commissure cut. 2mm.
684) *Helicigona lapicida,* pulmonary complex. 7.4mm.
685) *Helicigona lapicida,* nervous system in dorsal view. 2mm.
686) *Idem,* cerebral commissure cut. 2mm.

680



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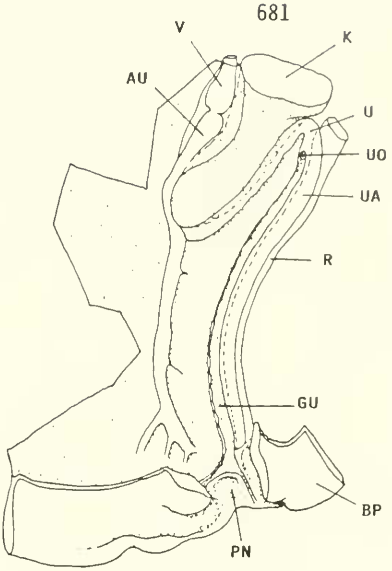

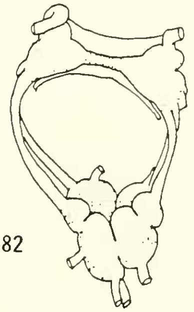

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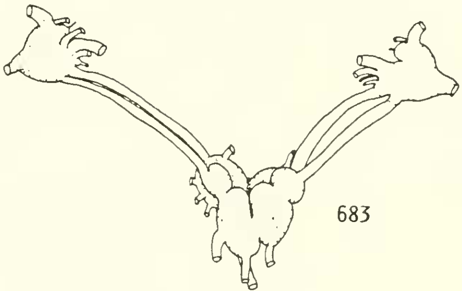

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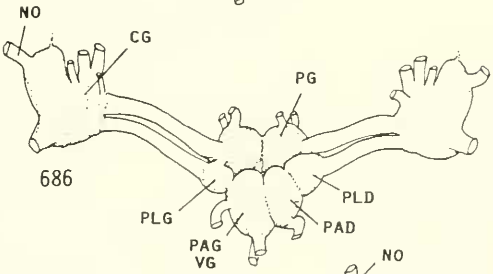

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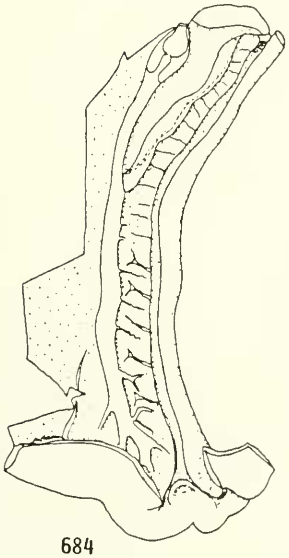

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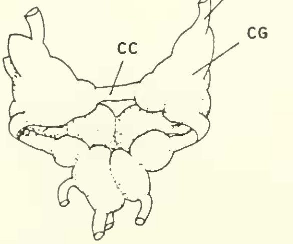

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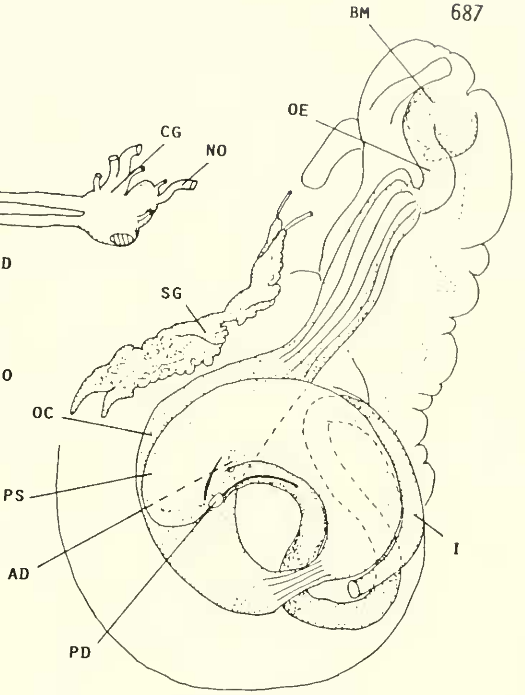
FIGS. 687–692: HELICIDAE (CAMPYLEINAE)
687) *Elona quimperiana*, digestive tract. 7.6mm.
688) *Elona quimperiana*, nervous system in dorsal view. 2.5mm.
689) *Idem*, cerebral commissure cut. 2.5mm.
690) *Elona quimperiana*, pulmonary complex. 10.4mm.
691) *Elona quimperiana*, kidney internal morphology. 6.2mm.
692) *Theba pisana*, pulmonary complex. 8.1mm.

687



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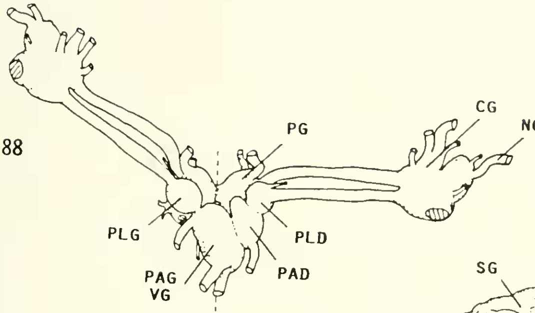

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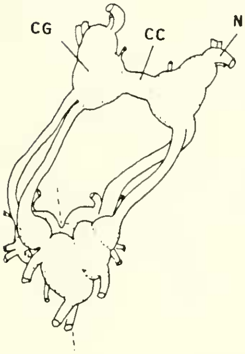

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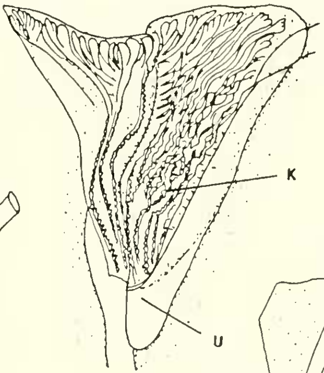

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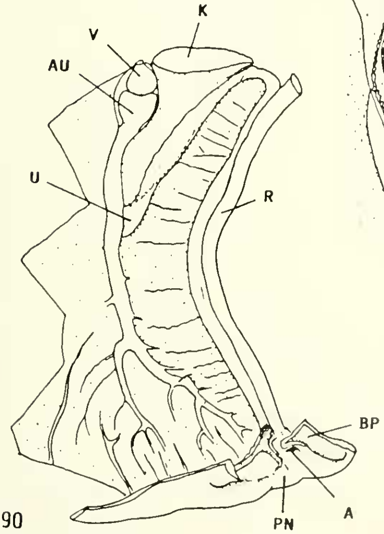

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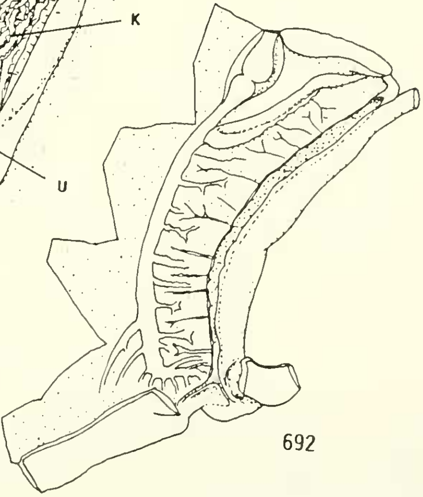
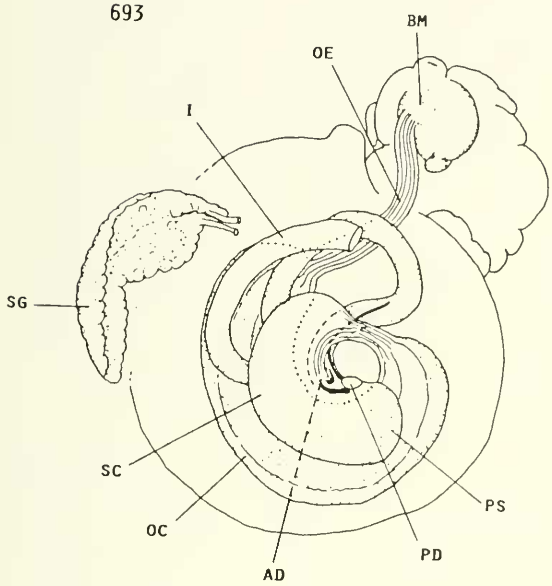


FIGS. 693–698: HELICIDAE (CAMPYLEINAE, HELICINAE)
693) *Arianta arbustorum*, digestive tract. 5.9mm.
694) *Arianta arbustorum*, nervous system in dorsal view. 2.5mm.
695) *Idem*, cerebral commissure cut. 2.5mm.
696) *Arianta arbustorum*, pulmonary complex. 10.8mm.
697) *Helix aspersa*, nervous system in dorsal view. 4.6mm.
698) *Idem*, cerebral commissure cut. 4.6mm.

693



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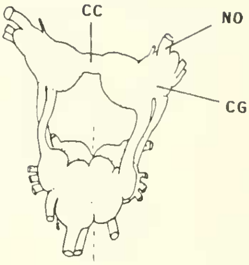

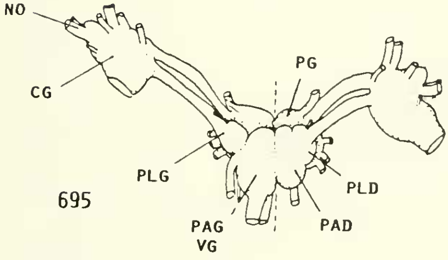

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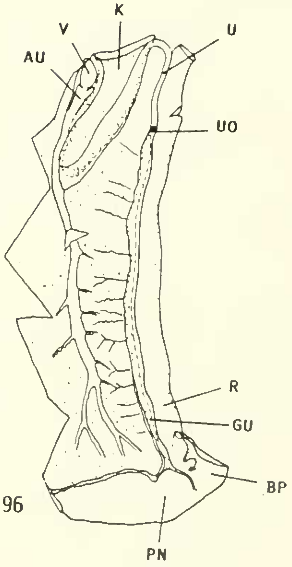

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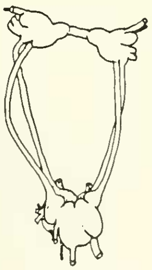

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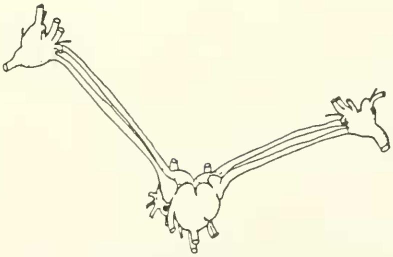
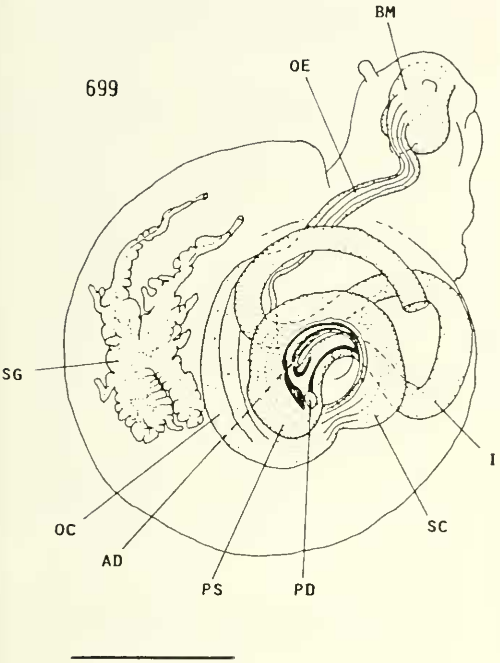


698

FIGS. 699–704: HELICIDAE (HELICINAE)
699) *Cepaea nemoralis*, digestive tract. 9.7mm.
700) *Cepaea nemoralis*, nervous system in dorsal view. 2.5mm.
701) *Idem*, cerebral commissure cut. 2.5mm.
702) *Cepaea nemoralis*, pulmonary complex. 19.4mm.
703) *Cepaea nemoralis*, kidney internal morphology. 6.7mm.
704) *Helix aspersa*, pulmonary complex. 19.4mm.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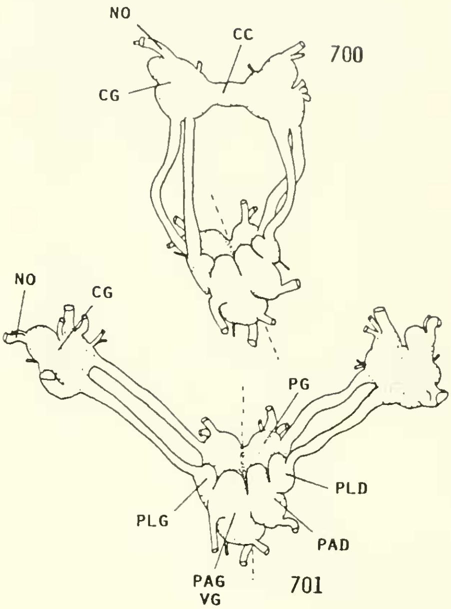
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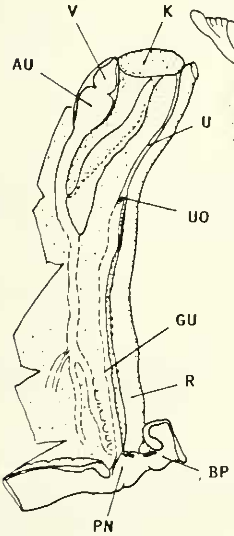
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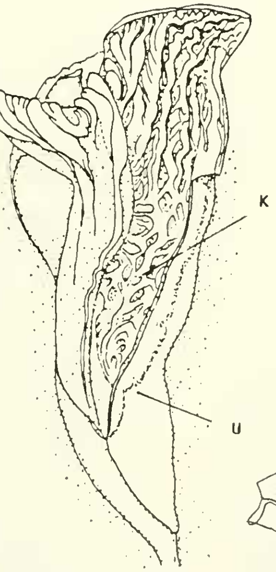
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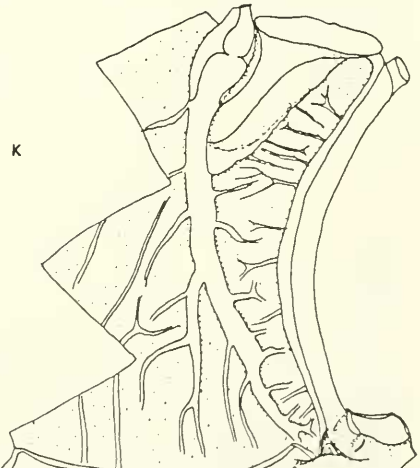
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APPENDIX A. MATERIAL STUDIED, ABBREVIATIONS USED IN TEXT-FIGURES

The order of presentation follows Zilch (1959–1960). Each family and some subfamilies are numbered in this order; fossil families, and a few Recent families are not represented. Each species is abbreviated by three or four signs, the first of them being the number of the family or subfamily (Text-figs. 6, 7). The systematic position adopted in the present work is indicated in parentheses.

Acronyms are: AMS = Australian Museum, Sydney; ANSP = Academy of Natural Sciences, Philadelphia; BMNH = British Museum (Natural History), London; FMNH = Field Museum of Natural History, Chicago; MNHN = Muséum national d'Histoire naturelle, Paris; MRAC = Musée Royal de l'Afrique centrale, Tervuren; RMNH = Rijksmuseum van natuurlijke Historie, Leiden; ZMA = Zoological Museum, Amsterdam

1–2 ACHATINELLIDAE (+ Zilch's Tornatellinidae; Orthurethra, Pupilloidea)

Auriculellinae

1Aur: *Auriculella auricula* (Férussac). Mt. Tantalus, Manoa Cliff Trail 2, Oahu, Hawaii. Solem! XII.16.1961. FMNH 166368.

1Aup: *Auriculella pulchra* (Pease). Kulau Crest, 500–600m, Kalihi Valley, Oahu, Hawaii. Solem & Kondo! XII.1961. FMNH 155351.

1Ela: *Elasmias* sp. Fautaua valley, Tahiti. Solem! I.9.1962. FMNH 155306.

1Lam: *Lamellidea* cf. *pusilla* (Gould). Fautaua valley. Tahiti. Solem! I.7.1962. FMNH 155283.

Tornatellininae

1Tor: *Tornatellides oblongus oblongus* (Anton). Musée Gauguin, Papeare, Tahiti. Solem! IV.18.1974. FMNH 182057.

1Str: *Strobilus plicosa* (Ohdner). Portuazela, Masatierra, Juan Fernandez. Malkyn! 7.IV.1962. FMNH 167976.

1Tek: *Tekoulina pricei* Solem. Summit of Mt. Te Kou, 630m, Rarotonga, Cook Islands. Price! 9.XII.1965. FMNH 153414.

2 Achatinellinae

2Ach: *Achatinella lorata* (Férussac). Slopes of Mt. Tantalus, Oahu, Hawaii. Solem! FMNH.

3 PARTULIDAE (Orthurethra, Partuloidea)

3Par: *Partula caledonica* Pfeiffer. Forest along coast, 20km SE of Port Vila, Efate, Vanuatu. Price! 2.X.1972. FMNH.

3Eua: *Eua expansa* (Pease). Mt. Solau, Upolu, Western Samoa. Solem & Price! 8.II.1965. FMNH 152889.

3Sam: *Samoana conica* (Gould). Pago-Pago, Fagasa Pass, Tutuila, Samoa. Price! 13.III.1975. FMNH 181061.

4 AMASTRIDAE (Orthurethra, Chondrinoidea)

Leptachatininae

4Lep: *Leptachatina balteata* (Pease). Kalalau trail, Pali-Kona, NE Kauai, Hawaii. Price! 2.IV.1975. FMNH 181168.

Amastrinae

4Ama: *Amastra pullata umbrata* Baldwin. Puukolekole. ANSP 108656.

5 COCHLICOPIDAE (Orthurethra, Chondrinoidea)

5Coc: *Cochlicopa lubrica* (Müller). Louisville, Kentucky, USA. Tillier! 12.IX.1981. MNHN.

6 PYRAMIDULIDAE (Orthurethra, Pupilloidea)

6Pyr: *Pyramidula rupestris* (Draparnaud). Marigna-sur-Valouse, Jura, France. Bouchet! 3.X.1976. MNHN.

7 VERTIGINIDAE (Orthurethra, Chondrinoidea)

Truncatellininae

7 Bot: *Bothriopupa breviconus* Pilsbry. St-Georges de l'Oyapock, French Guyana. Geay! 1900. MNHN.

Nesopupinae

7Ste: *Sterkia eyriesii* (Drouët). Régina, French Guyana. Tillier! 25.IV.1977. MNHN.

8 ORCULIDAE (Orthurethra, Chondrinoidea)

8Orc: *Orcula dolium dolium* (Draparnaud). Georges du Moutier, 250m, canton de Berne, Switzerland. Gittenberger! 22.V.1971. RMNH 2314.

8Pag: *Pagodulina serveri* (Zilch). St-Cézaire sur Siagne, 240m, Alpes-maritimes, France. Gittenberger! V.1976. RMNH.

9 CHONDRINIDAE (Orthurethra, Chondrinoidea)

Chondrininae

9Sol: *Solatopupa similis* (Bruguière). Sommières, Gard, France. Boulinier! III.1972. MNHN.

Hypselostomatinae

9Gyl: *Gyliotrachela depressispira* Van Benthem Jutting. Bukit Chintamani, Pahang, Malaysia. Berry! 1.II.1960. ZMA.

10 PUPILLIDAE (Orthurethra, Pupilloidea)

Pupillinae

10 Pup: *Pupilla muscorum* (L.). Berck, Pas-de-Calais, France. Chevallier! 21.X.1970. MNHN.

Lauriinae

10Lau: *Lauria cylindracea* (Da Costa). Box Hill, Surrey, England. BMNH.

11 VALLONIIDAE (Orthurethra, Pupilloidea)

Valloniinae

11Val: *Vallonia albula* Sterki. Bethlehem, South Dakota, USA. Tillier! 6.IX.1981. MNHN.

Acanthinulinae

11Pty: *Ptychopatula dioscoricola insigne* (Pilsbry). Confluence of rivers Courouaïe and Oyapock, French Guyana. Tillier! 2.V.1977. MNHN.

11Aca: *Acanthinula aculeata* (Müller). Bladafval, Azores. Backhuys! 13.VI.1969. RMNH 2339.

11Spe: *Spermodea lamellata* (Jeffreys). Burnham Beeches, Buckinghamshire, England. 20.V.1962. BMNH.

Spelaeodiscinae

11Klem: *Klemmia magnicosta* Gittenberger. Cna Gora; Comarro, Yugoslavia. Gittenberger! V.1975. RMNH 2426.

Strobilopsinae

11Str: *Strobilops aenea* Pilsbry.1- Rockville, Parke Co., Indiana, USA. Dybas & Kethley! 16.VI.1972. FMNH 170108. 2- Pine Hills, Union Co., Illinois, USA. Solem & Kethley! 14.X.1975. FMNH 171612

12 PLEURODISCIDAE (not seen)

13 ENIDAE (Orthurethra, Partuloidea)

Chondrulinae

13Cho: *Chondrula tridens* (Müller). Meximieux, Ain, France. Chevallier! 3.V.1971. MNHN.

Jamininae

13Imp: *Imparietula jousseaumei* (Smith). Jabal Akhdar, Oman. 22.V.1981. BMNH.

Eninae

13 Ena: *Ena montana* (Draparnaud). Cirque du Fer, 995m, Cheval, Haute-Savoie, France. Chevallier! 7.VII.1969. MNHN.

Zebrina eburnea (Pfeiffer). Tarsus, "Iran" (Turkey?). 28.VI.1961. BMNH.

Cerastuinae

13Rach: *Rachistia histrio* (Pfeiffer). La Roche, Maré, Loyalty Islands, New Caledonia. 7.X.1958. FMNH 109435.

13Cer: *Cerastua somaliensis* (Smith). Salan Gudun, Somalia. BMNH.

13Ami: *Amimopina macleayi* (Brazier, 1876). Cape York Peninsula, Australia. Wassell! 15.III.1959. FMNH.

13Dra: *Draparnaudia michaudi* (Montrouzier). Hienghène, New Caledonia. Price! 13.X.1967. FMNH 159299.

14 SUCCINEIDAE (Dolichonephra, Achatinoidea)

Catinellinae

Succineinae

14Suc: *Succinea putris* (L.). Le Hade, Seine-maritime, France. Chevallier! 29.IX.1967. MNHN.

14Su2: *Succinea propinqua* Drouët. Ilet le Père, French Guyana. Geay! MNHN.

14Hya: *Hyalimax perlucidus* (Quoy & Gaimard). Forêt de Saint-Philippe, La Réunion. Lantz! MNHN.

14Oma: *Omalonyx matheroni* (Potiez & Michaud). 17km SE of Kourou, French Guyana. Tillier! 1978. MNHN.

15 ATHORACOPHORIDAE (Brachynephra, Endodontoidea)

15Ane: *Aneitea simrothi* Grimpe & Hoffmann. Thiem, 10–50m. New Caledonia. Bouchet! 25.XII.1978. MNHN.

15Ath: Athoracophoridae sp. Vallée d'Amoa, 20m, New Caledonia. Tillier, Tillier & Mordan! 18.I.1981. MNHN.

16 ENDODONTIDAE (Brachynephra, Endodontoidea)

16Tha: *Thaumatodon hystricelloides* (Mousson). Mt. Lanuto, 830m, Upolu, Western Samoa. Price! 12.I.1965. FMNH.

16Lib: *Libera fratercula rarotongensis* Solem. Paratype. E of Avarua, Rarotonga, Cook Islands. Price! 7.XII.1965. FMNH.

17 CHAROPIDAE (Brachynephra, Endodontoidea)

17 Tra: *Trachycystis (Xerocystis) capensis* (Pfeiffer). Mainland River, Cape Province, South Africa. Van Bruggen! 2.IV.1961. RMNH.

17Cha: Charopidae sp. Mt. Toolbrunup, N of Albany, Western Australia. Solem! 19.IV.1980. FMNH 204670.

17Ann: *Annoselix dolosa* (Iredale). Oakley Dam, Darling Range, Western Australia. Solem & Price! 10.II.1974. FMNH 182229.

17Lui: *Luinodiscus* sp. Yallingup Caves, W of Busselton, Western Australia. Solem & Price! 10.II.1974. FMNH 182179.

17Pse: *Pseudocharopa lidgbirdi* Etheridge. Mt. Lidgbird, 500m, Lord Howe Island. Price! IX.1963. FMNH 127977.

17Mys: *Mystivagor mastersi* (Brazier). Mt. Lidgbird, 400m, Lord Howe Island, Price! IX.1963. FMNH 127963.

17Ran: *Ranfurlya constanceae* Suter. Musgrave Peninsula, Auckland, New Zealand. 15.XI.1943. Auckland Museum.

17Par: *Pararhytida dictyodes* (Pfeiffer). Numerous localities, New Caledonia. Cf. Tillier & Mordan, 1986.

17Pa2: *Pararhytida marteli* (Dautzenberg). Numerous localities, New Caledonia. Cf. Tillier & Mordan, 1986.

17Pa3: *Pararhytida mouensis* (Crosse). Numerous localities, New Caledonia. Cf. Tillier & Mordan, 1986.

17And: *Andrefrancia* sp. Mt. Mou, 450m, New Caledonia. Mordan, Tillier & Tillier! 5.I.1981. MNHN.

17Ste: *Stephanoda binneyana* (Pfeiffer). Rio Cisnes, Aysen, Chile. Pena! II.1961. FMNH 135428.

18 PUNCTIDAE (Brachynephra, Endodontoidea)

18Cys: *Cystopelta purpurea* (Davies). Mt. Donna Buang, 1350m, Great Dividing Range, Victoria, Australia. Solem! FMNH 182252.

18Par: *Paralaoma lateumbilicata* (Suter). South West Island, Three Kings Islands, New Zealand. Price! I.1963. FMNH.

18Phr: *Phrixgnathus erigone* (Gray). Waitakere Range, North Island, New Zealand. Price! FMNH 135477.

18Lao: *Laoma leiomonas* (Gray). Herekina Gorge, S of Kaitaia, North Island, New Zealand. Price! XI.1962. FMNH 135401.

19 DISCIDAE (Dolichonephra, Zonitoidea)

Discinae

19Dis: *Discus rotundatus* (Müller). Hendaye, Basses-Pyrénées, France. Chevallier! 27.VII.1968. MNHN.

19Di2: *Discus patulus* (Deshayes). Bixby State Park, Clayton Co., Iowa, USA. Solem! 18.VI.1974. FMNH 171131.

19Ang: *Anguispira alternata* (Say). Grundy Co., Illinois, USA. Burke! 31.II.1965. FMNH 153221.

19An2: *Anguispira macneilli* Clapp. Tombigbee River, Leroy, Washington Co., Alabama, USA. Hubricht! 3.VII.1960. FMNH 170671.

Helicodiscinae

19Hel: *Helicodiscus parallelus* Say. Raymond Cave, Fulton Co., Arkansas, USA. Barnett! 10.V.1969. FMNH 173668.

20–21 ARIONIDAE (+ Zilch's Philomycidae; Dolichonephra, Zonitoidea)

Binneyinae

20Hem: *Hemphillia camelus* Pilsbry & Vanatta. Rye Patch Creek, 700m, Lochsa River, Idaho Co., Idaho, USA. FMNH 97995.

Ariolimacinae

20Ari: *Ariolimax columbianus* (Gould). Myrtle Grove State Park, Curry Co., Oregon, USA. Dybas! 22.V.1957. FMNH 193553.

20Aph: *Aphallarion buttoni* Pilsbry & Vanatta (= *Ariolimax columbianus?*: Pilsbry, 1948). Oakland, California, USA. Button! 1.VIII.1896. ANSP A2864.

20Zac: *Zacoleus idahoensis* Pilsbry. Kootenai Falls, Montana, USA. Forrester! 17.IX.1959. FMNH 117624.

20Hes: *Hesperarion niger* (Cooper). Brown's Ravine, Folsom Lake State Park, Sacramento Co., California, USA. Smith & Solem! 9.IV.1960. FMNH 98045.

Anadeninae

20Pro: *Prophysaon humile* Cockerell. Rye Patch Creek, 700m, Lochsa River, Lowell, Idaho Co., Idaho, USA. Walton & Solem! 24.IV.1960. FMNH 98095.

Arioninae

20Ari: *Arion rufus* (L.). Confranc, Huesca, Spain. Alvarez! VII.1971. MNHN.

20Geo: *Geomalacus maculosus* Allman. Glengariff, W of Cork, Ireland. Quick! VIII.1931. RMNH 4125.

Oopeltinae

20Oop: *Oopelta granulosa* Collinge. Nieuwoudtville, Willems River, Cape Province, South Africa. Visser & Kotzé! 2.IX.1980. ANSP A9361.

20Oo2: *Oopelta nigropunctata* Mörch. Capetown, South Africa. Collinge! 23.IV.1909. University Museum, Cambridge.

21 Philomycinae

21Phi: *Philomycus carolinianus* (Bosc). Cumberland Falls, McCreary Co., Kentucky, USA. Solem! 16.VI.1954. FMNH 198648.

21Ph2: *Incillaria (= Philomycus?) bilineata* Benson. Isushima (?). BMNH 1903.5.22.33.

22 THYROPHORELLIDAE (not seen)

23 VITRINIDAE (Dolichonephra, Zonitoidea)

23Phe: *Phenacolimax major* (Férussac). Les Egletons, Corrèze, France. Chevallier! 22.IV.1967. MNHN.

23Ph2: *Phenacolimax? ugandensis* (Thiele). Kimakia, 2700m, Kenya. Verdcourt! 14.IV.1963. BMNH.

23Plu: *Plutonia atlantica* (Morelet). Rosaias, São Jorge Island, Azores, Backhuys! RMNH 2339.

24 ZONITIDAE (Dolichonephra, Zonitoidea)

Vitreinae

24Vit: *Vitrea crystallina* (Müller). Box Hill, Surrey, England. Peake! V.1960. BMNH.

Zonitinae

24Mes: *Mesomphix inornatus* (Say). Elkton, NNW of Charlottesville, Virginia, USA. Hopman! 29.V.1982. FMNH.

24Aeg: *Aegopinella nitidula* (Draparnaud). Nogent-sur-Seine, Aube, France. Cayet! 1980. MNHN.

24Zon: *Zonites algirus* (L.). Nîmes, Gard, France. Testud! 7.IV.1976. MNHN.

24Oxy: *Oxychilus draparnaudi* (Beck). Gournay-sur-Marne, France. Chevallier! 3.XI.1974. MNHN.

Daudebardiinae

24Dau: *Daudebardia lederi* Boettger. Caucasus. BMNH 86.3.11.114.

24Da2: *Daudebardia* sp. Hamsikoï, 1900m, 45km. SSW of Trabzon, Turkey. Vader! 5.VI.1959. RMNH 1583.

Gastrodontinae

24Ven: *Ventridens acera* (Lewis), Buck Creek Cove, Sherwood, Franklin Co., Tennessee, USA. Goodfriend! 6.IX.1974. FMNH 171144.

24Zon: *Zonitoides arboreus* (Say). Hertfordshire, England. BMNH.

Gastrodonta interna (Say). Handpole Brook, Nantahala Gorge, Macon Co., North Carolina, USA. FMNH 171325.

25 PARMACELLIDAE (Dolichonephra, Zonitoidea)

25Par: *Parmacella valenciennesi* Webb & Berthelot. Loulé, Algarve, Portugal. Coiffait! 1970. MNHN.

25Pa2: *Parmacella deshayesi* Moquin-Tandon. Algeria, Marés! 1876. MNHN.

26 MILACIDAE (Dolichonephra, Zonitoidea)

26Mil: *Milax gagates* (Draparnaud). France, laboratory grown. Chevallier! MNHN.

27 LIMACIDAE (Dolichonephra, Zonitoidea)

27Lim: *Limax maximus* L. St. Martin-de-Vésubie, 960m, Alpes-maritimes, France. Chevallier! 31.VIII.1979. MNHN.

28 TRIGONOCHLAMYDIDAE (not seen; = Limacidae, Zonitoidea, Dolichonephra)

Trigonochlamydinae

Parmacellillinae

29 TROCHOMORPHIDAE (Dolichonephra, Zonitoidea)

29Tro: *Trochomorpha* sp. Mt. Kinabalu, 3100–3300m, Sabah, Borneo, Malaysia. Bouchet! XII. 1980. MNHN.

30 EUCONULIDAE (Dolichonephra, Zonitoidea)

30Con: *Conibycus dahli* Thiele. Rô, Maré, Loyalty Islands, New Caledonia. Bouchet! 8.VI.1978. MNHN.

30Dis: *Discoconulus* sp.1. Mt. Kinabalu, 3100–3300m, Sabah, Borneo, Malaysia. Bouchet! XII.1980. MNHN.

30Di2: *Discoconulus* sp.2. same locality.

30Cop: *Coneuplecta* sp.1. same locality.

30Co2: *Coneuplecta* sp.2. same locality.

30Co3: *Coneuplecta* sp.3. same locality.

30Vit: *Vitrinopsis* sp.1. same locality.

30Vi2: *Vitrinopsis* sp.2. same locality.

31 HELICARIONIDAE (+ Zilch's Urocyclidae; Dolichonephra, Helicoidea)

Helicarioninae

31Kal: *Kalidos oleatus* (Ancey). Marojezy, 1300m, W of Sambava, Madagascar. Blanc! 1.XII.1972. MNHN.

31Mal: *Malagarion paenelimax* Tillier. Holotype, Marojezy, 600m, Madagascar. Blanc! 12.XII.1972. MNHN.

31Hel: Helicarionidae sp. Poindimié, New Caledonia. Bouchet! 29.XII.1978. MNHN.

Dyakiinae

31Eve: *Everettia corrugata* Laidlaw. Mt. Kinabalu, 3100-3300m, Sabah, Borneo, Malaysia. Bouchet! XII.1980. MNHN.

Ariophantinae

31Par: *Parmarion martensi* Simroth. Cambodia. Harmand! 1875. MNHN.

31Mic: *Microparmarion pollonerai* Collinge & Godwin-Austen. Mt. Kinabalu, 3100 m, Sabah, Borneo, Malaysia. Bouchet! 13.1.1981. MNHN.

31Hem: *Hemiplecta humphreysiana* (Lea). Sengel Kumbang, 1600m, Korinchi, Sumatra, Malaysia. BMNH.

31Mar: *Mariaella dussumieri* Gray. Mahé, India. Dussumier! 1835. MNHN.

Trochozonitinae

31Tro: *Trochozonites percarinatus* Von Martens. 10km from Buea, road to Tiko, Zaïre. Van Mol! 2.IX.1968. MRAC 795610.

Gymnarioninae

31 Gym: *Gymnarion sowerbyanus* (Pfeiffer). Assinie, Ivory Coast. Chaper! 1882. MNHN.

31Aca: *Acantharion browni* Binder & Tillier. Paratypes, Tississat Falls, Blue Nile, Ethiopia. Brown & Posser! 22.VIII.1965. MNHN.

Urocyclinae

31Elg: *Trochonanina (Montanobloyetia) simulans meruensis* Verdcourt. Mt. Meru, 1700m, Tanzania. Ross & Leech! 28.X.1957. FMNH 106125.

31Mes: *Mesafricarion maculifer* Pilsbry. Lodjo, Mongbwalu, Zaïre. Lepersonne! VIII.1939. MRAC.

31Gra: *Granularion lamottei* Van Mol. Mt. Nimba, Guinea, Lamotte! 1956. MNHN.

31Est: *Estria?* sp.A (cf. Van Goethem, 1977: 87). Gopoupleu, Ivory Coast, Condamin & Roy! 1959. MNHN.

31Tre: *Tresia parva* Van Goethem. Paratypes, Mt. Nimba, Guinea. Lamotte! 1956–1957. MNHN.

31Eli: *Elisolimax madagascariensis* (Poirier). Montagne d'Ambre, Diego Suarez, Madagascar. Salvat & Blanc! 1970. MNHN.

31Ato: *Atoxon pallens* Simroth. Virunga, Zaïre. Vanschuytbroek! 1954. MNHN.

32 FERUSSACIIDAE (Dolichonephra, Achatinoidea)

32Cae: *Cecilioides acicula* (Müller). Los Blanos, 350m, La Palma, Canary Islands. V.R. Altena! 27.IV.1947. RMNH 705.

33 SUBULINIDAE (Dolichonephra, Achatinoidea)

Subulininae

33Sub: *Subulina octona* (Bruguière). Poum, New Caledonia. Bouchet! 16.V.1979. MNHN.

33Boc: *Bocageia carpenteri* Connolly. Kitala, 2500m. Mt. Elgon, Zaïre. Bouillon! 5.XII.1953. MRAC 6118117.

33Pse: *Pseudoglessula hessei* (Boettger). Banryville, Zaïre. Wanson! IX.1949. MRAC 315164.

Rumininae

33Rum: *Rumina decollata* (L.). Aleria, Corsica, France. Monniot! IV.1980. MNHN.

34 ACHATINIDAE (Dolichonephra, Achatinoidea)

34Ach: *Achatina fulica* Bowdich. Noloina, Tamatave, Madagascar. Pointel! 1964. MNHN.

35 MEGASPIRIDAE (not seen; Brachynephra, Clausilioidea?)

36 FILHOLIIDAE (fossil; Brachynephra, Clausilioidea?)

37 CLAUSILIIDAE (Brachynephra, Clausilioidea)

Neniinae

37Nen: *Nenia tridens* (Schweigger). Catano, Puerto Rico. Baker! ANSP A1929.

Alopiinae

37Alb: *Albinaria olivieri* (Roth). Filerimos, Rhodes, Greece. Riedel! 23.IV.1980. FMNH.

37Ita: *Itala itala* (von Martens). Sommières, Gard, France. Boulinier! III.1972. MNHN.

38 OLEACINIDAE (+ Zilch's Testacellidae; Dolichonephra, Achatinoidea)

Spiraxinae

38Spi: *Spiraxis futilis* Baker. Nexaca, Mexico. ANSP A1908.

Oleacininae

38Var: *Varicella biplicata dissimilis* Pilsbry. J20, SW VII.25.23 (?). ANSP A1860.

38Poi: *Poiretia dilatata* (Philippi). Sicily. Caron! 1836. MNHN.

38 Str: *Streptostyla streptostyla* (Pfeiffer). Sumidero, Mexico. 25.VI.1926. ANSP A1855.

38Eug: *Euglandina carminensis* (Morelet). Starr Creek Valley, Honduras, Sanderson! 17.I.1940. BMNH.

38Stb: *Strebelia berendti* (Pfeiffer). Texolo, Vera Cruz, Mexico. Rhoades! 1899. ANSP A1924A.

39 Testacellinae (= Oleacinidae, Achatinoidea, Dolichonephra)

39Tes: *Testacella haliotidea* Draparnaud. Montlhéry, Essonne, France. MNHN.

40 ACAVIDAE (Brachynephra, Acavoidea)

40Tri: *Trigonephrus rosaceus minor* Connolly. Namaqualand, South Africa. Connolly! VI.1924. University Museum, Cambridge.

40Dor: *Dorcasia alexandri* Gray. Vaalgrass Farm, Khomas Hochland, Namibia. Lavranos! MNHN.

40Str: *Strophocheilus chilensis* (Sowerby). Manquehua, Coquimbo, Chile. Pena! X.1961. FMNH 121481.

40Ped: *Pedinogyra* sp. Mt. Dryander, 16km NE of Proserpina, North Queensland, Australia. Price! 18.XI.1971. FMNH.

40Hed: *Hedleyella falconeri* (Reeve). Hortons Creek, S. of Nymboida, New South Wales, Australia. Price! 20.X.1971. FMNH 173554.

40Pyg: *Hedleyella (Pygmipanda) kershawi* (Brazier). 11km N of the lakes, Victoria, Australia. Price! 19.X.1968. FMNH 160038.

40Ano: *Anoglypta launcestonensis* (Reeve). Myrtle Bank, NE Tasmania. Dartnell! XI.1972. FMNH 170413.

40Car: *Caryodes* sp. Ouse River bridge near the Great Lake, central Tasmania. Price! 18.X.1968. FMNH 154857.

40Pan: *Pandofella whitei* (Hedley). Eungella State Park, 800m, 80km W of Mackay, North Queensland, Australia. Price! 15.XI.1971.

40Pad: *Panda larreyi* (Brazier). Near Dorrigo, 900m, NE New South Wales, Australia. Price! 23.X.1971.

40Mac: *Macrocyclis laxata* (Férussac). W. of Ancud, Chiloe island, Chile. Engel! 2.II.1976. FMNH 206301.

40Amp: *Ampelita petiti* Fischer-Piette. W of the Ibory, Madagascar. Blanc! 15.XII.1970. MNHN.

40Hel: *Helicophanta vesicalis* Lamarck. Ste Luce forest, Madagascar. Blanc! 9.XII.1971. MNHN.

40Cla: *Clavator eximius* Shuttleworth. Anjavidilava, Madagascar. Blanc! 8.I.1971. MNHN.

40Sty: *Stylodon studerianus* (Férussac).

Vallée de Mai, Mahé, Seychelle Islands. Hunon! 1979. MNHN.

40Aca: *Acavus superbus* (Pfeiffer). Ceylon. Dobell! 11.XI.1909. University Museum, Cambridge.

41 BULIMULIDAE (+ Zilch's Odontostomidae and Orthalicidae; Brachynephra, Clausilioidea)

Bulimulinae

41Bos: *Bostryx bermudezae* Weyrauch. Quichero, Valley of Rio Canete, Province of Lima, Peru. Breure! 6.II.1975. RMNH 2605.

41Coc: *Cochlorina aurisleporis* (Bruguière). Linhares, Espiritu Santo, Brazil. Elias! XII.1972. RMNH 2629.

41Pla: *Placostylus fibratus* (Martyn). Kouto, Ile des Pins, New Caledonia. Bouchet! 15.VIII.1978. MNHN.

41Dis: *Discoleus azulensis* (Döering). Sierra de Lihuelcalal, La Pampa, Argentina. Hylton Scott! RMNH.

41Sim: *Simpulopsis miersi* Pfeiffer. Linhares, Espiritu Santo, Brazil. Domingos! I.1972. RMNH 9036.

Amphibuliminae

41Pel: *Pellicula depressa* (Rang). La Soufrière, 1100m, La Guadeloupe. Tillier! 26.III.1983. MNHN.

Odontostominae

41Plg: *Plagiodontes daedaleus* (Deshayes). Cerro del Moro, San Luis, Argentina. Castellanos! 1949. RMNH 3698.

41Ano: *Anostoma depressa* Lamarck. Baixa Verde, Brazil. ANSP 109325.

42 ANADROMIDAE (fossil)

43 CERIONIDAE (Brachynephra, Clausilioidea)

43Cer: *Cerion copium* Maynard. Cayman Brac. Hummelinck! 1.VI.1973. MNHN.

43Ce2: *Cerion casablancae* Bartsch. Andros, Bahamas. Gould & Woodruff! MNHN.

44 UROCOPTIDAE (Brachynephra, Clausilioidea)

Eucalodiinae

44Ber: *Berendtia taylori* (Pfeiffer). Mission of San Javier, 1300m, Baja California Sur, Mexico. Christensen! 25.X.1972. RMNH.

Urocoptinae

44Mac: *Macroceramus signatus* (Guilding). Anegada, Virgin Islands. FMNH 151675.

44Uro: *Urocoptis procera* (Adams). Near Windsor Cave, Windsor, Trelawny, Jamaica. Goodfriend! 28.VII.1974. FMNH 196515.

45 SYSTROPHIIDAE (Brachynephra, Endodontoidea)

45Sys: *Systrophia (Systrophiella) eudiscus* Baker. Sierra de Perija, El Roncon, E of Becerril, Cesar, Colombia. 16.IX.1969. FMNH 167951.

45Sy2: *Systrophia (Wayampia) cayennensis* (Pfeiffer). Kaw, French Guyana. Tillier! 29.IV.1977.

45Tam: *Tamayoa decolorata* (Drouët). Saut Sabbat, French Guyana. Tillier! 13.V.1977. MNHN.

46 HAPLOTREMATIDAE (Dolichonephra, Helicoidea)

46Hap: *Haplotrema concavum* (Say). Louisville, Kentucky, USA. Tillier! 12.IX.1981. MNHN.

46Ha2: *Haplotrema minimum* (Ancey). Alameda Co., California, USA. 9.IV.1960. FMNH 98105.

47 RHYTIDIDAE (+ Zilch's Chlamydephoridae; Brachynephra, Acavoidea)

47Pri: *Priodiscus serratus* Adams. Mahé, Seychelle Islands. Benoît & Van Mol! 8.VIII.1972. MRAC 798907.

47Oua: *Ouagapia raynali* (Gassies). Col de Petchékara, 400–450m, New Caledonia. Bouchet! 18.XI.1978.

47Dip: *Diplomphalus megei* (Lambert). Forêt Nord, New Caledonia. Mordan, Tillier & Tillier! 21.I.1981. MNHN.

47Rhy: *Rhytida inaequalis* (Pfeiffer). Monéo, New Caledonia. Bouchet! 15.V.1978. MNHN.

47Nat: *Nata* cf. *vernicosa* (Krauss). Pietermaritzburg, Natal, South Africa. Kellsall! 9.IV.1963. MNHN.

47Sch: *Schizoglossa novoseelandica* Pfeiffer. Egmont, New Zealand. Murdoch! BMNH 94.10.30.1.

48 Chlamydephorinae (= Rhytididae, Acavoidea, Brachynephra)

48Chl: *Chlamydephorus gibbonsi* (Binney). Cape Province, South Africa. Neale! BMNH 79.6.25.1.

49 STREPTAXIDAE (Dolichonephra, Achatinoidea)

49Ede: *Edentulina* sp. Esten Province, Kenya. Charles! 22.V.1971. MRAC 140766.

49Gon: *Gonaxis enneoides* (von Martens). Marangu, 1550m, Kilimandjaro, Tanzania. Basilensky & Leloup! 27.II.1956. MRAC 7890055.

49Pty: *Ptychotrema* sp. Soyo Matadi, Zaïre. Dartevelle! II.1937. MRAC 211492.

50 POLYGYRIDAE (Dolichonephra, Helicoidea)

Polygyrinae

50Pol: *Polygyra matermontana jaliscoensis* (Pilsbry). Casa Helena, 5000m, Chapala, Jalisco, Mexico. deVry! XI.1963. FMNH 145705.

50Mes: *Mesodon andrewsae normalis* (Pilsbry). Near Ocoll, 300m, Polk Co., Tennessee, USA. Goodfriend! 2.IX.1974. FMNH.

50Tri: *Trilobopsis trachypepla* Berry. Eel River, Humboldt Co., California, USA. Solem! 12.IV.1960. FMNH 98097.

Triodopsinae

50Trd: *Triodopsis fraudulenta vulgata* Pilsbry. McGee Hill, Pine Hills, N of Wolf Lake, Union Co., Illinois, USA. Solem & Kandhley! 14.X.1975. FMNH 171598.

50All: *Allogona ptychophora* Brown. John Day Creek, N of Lucile, Idaho Co., Idaho, USA. Solem & Walton! 21.IV.1960. FMNH.

51 SAGDIDAE (Helicoidea, Dolichonephra)

51Sag: *Sagda* cf. *grandis*. Albert Town, Trelawny, Jamaica. Goodfriend! 12.VIII.1974. FMNH 196152.

51Lac: *Lacteoluna turbiniformis* (Pfeiffer). Corner Shop, Clarendon, Jamaica. Goodfriend! 28.VI.1974. FMNH 196079.

51Pro: *Proserpinula opalina* (Adams). Flint River, Hanover, Jamaica. Goodfriend! 30.VI.1974. FMNH 196104.

52 CORILLIDAE (Brachynephra, Acavoidea)

52Cor: *Corilla humberti* Brot. Ceylon, 2000m, Collett! ANSP 87433.

52Scu: *Sculptaria collaris* (Pfeiffer). Southern Angola. Gofas! 1982. MNHN.

52Ple: *Plectopylis* sp.1. Damsang Peak or Rissom Peak, 2000m, Malaysia, Robert! BMNH.

52Pl2: *Plectopylis* sp.2. Same sample.

52Cra: *Craterodiscus pricei* MacMichael. Hypipamee Crater, Atherton Tableland, Queensland, Australia. Price! VIII.1964. FMNH 135141.

53 CAMAENIDAE (Dolichonephra, Helicoidea)

53Ple: *Pleurodonte lychnuchus* (Müller). Maison de la Nature, Parc naturel, La Guadeloupe. Tillier! IV.1978. MNHN.

53Lab: *Labyrinthus leprieurii* (Petit). Trois Sauts, French Guyana. Tillier! 8.V.1978. MNHN.

53Sol: *Solaropsis undata* (Lightfoot). Trois Sauts, French Guyana. Tillier! V.1978.

53Rha: *Rhagada* sp. Mt. Hart Homestead, King Leopold Range, Western Australia. Price & Christensen! 13.XII.1976. FMNH 200050.

53Sin: *Sinumelon lennum* Iredale. Balladonia Hotel, NE of Esperance, Western Australia. Solem & Price! 21.II.1974. FMNH 182477.

53Amp: *Amplirhagada burnerensis* (Smith). Winjana Gorge, Napier Range, Western Australia, Price & Christensen! 21.III.1977. FMNH.

53Amd: *Amphidromus cognatus* Fulton. Milikapiti Bay, Melville Island, Northern Territories, Australia. AMS 126706.

53Plc: *Plectotropis goniocheila* (Pfeiffer). Kao Pra Put, Lop Buri, Thailand. Brandt! 24.X.1966. FMNH 155087.

54–55 OREOHELICIDAE (Brachynephra, Acavoidea)

54 Ammonitellinae

54Amm: *Ammonitella yatesi* Cooper. San Domingo Creek, Murphys, El Dorado Co., California, USA. Solem & Smith! 10.IV.1960. FMNH 98073.

54Gly: *Glyptostoma gabrielense* Pilsbry. Monrovia Canyon, San Gabriel Mts., Los Angeles Co., California, USA. Solem, Miller & Gregg! 3.IV.1960. FMNH 98041.

55 Oreohelicinae

55Ore: *Oreohelix barbata* Pilsbry. Cave Creek Canyon, Chiricahua Mts., Arizona, USA. Solem & Walton! 24.III.1960. FMNH 98103.

56 BRADYBAENIDAE (Dolichonephra, Helicoidea)

Helicostylinae

56Hel: *Helicostylus palawanensis* (Pfeiffer). Puerto Princesa, Palawan, Philippines. Hoogstraal! 19.IV.1947. FMNH 54961.

56Coc: *Cochlostyla melanocheila* (Pfeiffer). W. slope of Mt. Halcon, 400–600m, Mindoro oriental, Philippines. Bouchet! XII.1980. MNHN.

Bradybaeninae

56Bra: *Bradybaena tourannensis* (Eydoux & Souleyet). Lan Yu island, S of Hung Tsu Tsun, SE of Taiwan. Kuntz! III.1959. FMNH 82155.

57 HELMINTHOGLYPTIDAE (+ Zilch's Thysanophorinae; Dolichonephra, Helicoidea)

Xanthonycinae

57Ave: *Averellia coactiliata* (Deshayes). El Panden, Guatemala. McCarthy! 6.VIII.1976. FMNH 192826.

57Lep: *Leptarionta trigonostoma* (Pfeiffer). Montana del Mico, Isabal, Guatemala. Steyermark! 16.III.1940. FMNH.

Helminthoglyptinae

57Mon: *Monadenia fidelis* (Gray). Salyer, Trinity Co., California, USA. Talmadge! 13.IV.1960. FMNH.

57Hel: *Helminthoglypta sequoicola* (Cooper). Batchelder Ranch, Santa Cruz, California, USA. Strohbeen! 16.I.1960. FMNH 111545.

57Epi: *Epiphragmopora claromphalos* (Deville & Hupé). Quillabamba, 200m, Urubamba valley, Peru. Weyrauch! 1949. FMNH 30697.

Sonorellinae

57Son: *Sonorella walkeri* (Pilsbry & Ferriss). Gardner Canyon, Santa Rita Mts., Arizona, USA. Walton & Solem! 18.III.1960. FMNH.

Cepolinae

57Cep: *Cepolis varians* (Menke). French Leave, Eleuthera, Bahamas. Burke! 7.VII.1965. FMNH 147768.

57Ce2: *Cepolis maynardi* Pilsbry. South Bimini, Bahamas. Haas! 1.VIII.1956. FMNH 57104.

57Psa: *Psadara nubeculata* (Deshayes). Mt. St Marcel, 500m, French Guyana. Tillier! V.1978. MNHN.

57Ps2: *Psadara marmatensis* (Pfeiffer). Trois Sauts, French Guyana. Lescure! 1.IV.1976. MNHN.

Thysanophorinae

50Thy: *Thysanophora horni* (Gabb). Casa Helena, Chapala, Jalisco, Mexico. deVry! XI.1963. FMNH 145669.

58 HELICIDAE (Dolichonephra, Helicoidea)

Sphincterochilinae

58Sph: *Sphincterochila zonata* (Bourguignat). Near Massada, W of Dead Sea, Israel. Holthuis! 21.IV.1973. RMNH.

58Hal: *Halolimnohelix sericata lejeunei* Verdcourt. Paratype. Butembo, Kivu, Zaire. Lejeune! 1968. MRAC 794977.

Helicellinae

58Cer: *Cernuella virgata* (Da Costa). Claye- Souillis, Seine-et-Marne, France. Chevallier! 21.IX.1967. MNHN.

58Leu: *Leucochroa explanata* (Müller). La Grande Motte, Hérault, France. Testud! IV.1976. MNHN.

58Hec: *Helicella itala* (L.). S of Lincheux, Somme, France. Chevallier! 22.X.1970. MNHN.

58Tro: *Trochoidea elegans* (Gmelin) (= Hygromiinae?). Without locality, MNHN.

58Tr2: *Trochoidea geyeri* (Soos) (= Hygromiinae?). Langeray, Genève, Switzerland. Falkner! 1.III.1968. MNHN.

58Can: *Candidula unifasciata* (Poiret) (= Hygromiinae?). Between Ste-Affrique and St-Servin, Aveyron, France. Chevallier! 28.IV.1967. MNHN.

58Ca2: *Candidula intersecta* (Poiret) (= Hygromiinae?). Les Traverses, NE of Embrun, Hautes -Alpes, France. Chevallier! 25.VII.1969. MNHN.

58Hep: *Helicopsis striata* (Müller) (= Hygromiinae). Podersdorf, Burgenland, Austria. Clerx! VIII.1973. RMNH.

58He2: *Helicopsis* n.sp. (= Hygromiinae). Spain. RMNH.

58He3: *Helicopsis apicina* (Lamarck) (= Hygromiinae). Les Gondes, Cap Croisandte, Bouches-du-Rhône, France. Gittenberger! RMNH.

58Col: *Cochlicella acuta* (Müller) (=

Helicodontinae?). Deauville, Calvados, France, Chevallier! 1.X.1967. MNHN.

58Mon: *Monacha cartusiana* (Müller) (= Hygromiinae). Forêt de Sénart, Seine-et-Oise, France. Testud! 25.IX.1977. MNHN.

Hygromiinae

58Hyg: *Hygromia limbata* (Draparnaud). Chambre d'Amour, Pyrénées-Atlantiques, France. Chevallier & Deguirmenci! 6.IV.1966. MNHN.

58Tri: *Trichia hispida* (L.). Jardin des Plantes, Paris, France. Chevallier! 21.V.1969. MNHN.

Helicodontinae

58Hed: *Helicodonta obvoluta* (Müller). Georges de la Fou, Pyrénées-orientales, France. Tillier! 18.VII.1980. MNHN.

Campyleinae

58Elo: *Elona quimperiana* (Férussac). Ampuero, 50m, Santander, Spain. Bouchet! 21.VIII.1970. MNHN.

58Art: *Arianta arbustorum* (L.). Val du Giffre, 700m, Samoëns, Haute- Savoie, France. Chevallier! 5.VII.1969. MNHN.

58Heg: *Helicigona lapicida* (L.). Val du Hérisson, Jura, France. Chevallier! 1.VII.1969. MNHN.

Helicinae

58The: *Theba pisana* (Müller). Giberville, Calvados, France. Delaunay! 14.VIII.1969. MNHN.

58Cea: *Cepaea nemoralis* (L.). Toruy, Seine-Saint-Denis, France. Kassem! IX.1982. MNHN.

58Hel: *Helix aspersa* Müller. Sommières, Gard, France. Boulinier! III.1972. MNHN.

APPENDIX B. DATA (GENERAL MORPHOLOGY)
H, shell height; D, shell diameter; H/D, ratio; WH, whorl number of shell; TA, size rank; LV, whorl number of visceral mass; LP, lung length in whorls; ST, length in whorls of stomach above summit of lung; SS, length in whorls of visceral mass above summit of stomach; LS, total length in whorls of gastric crop and gastric pouch. Semislugs = 6000; slugs = 8000; missing data = 9999.

	H	D	H/D	WH	TA	LV	LP	ST	SS	LS
Auriculella auricula	4	2.4	1.66	4.5	22	3.75	1	1.25	1.5	1.3
Auriculella pulchra	9999	9999	9999	9999	9999	9999	9999	9999	9999	9999
Elasmias sp.	4.2	3	1.42	3.5	27	3.25	.8	1.2	1.25	1.2
Lamellidea sp.	3.4	1.9	1.83	6	20	4.75	1.1	1.6	2.05	1
Tornatellides oblongus	2.9	1.8	1.62	5	12	4.25	1.25	1	2	1.3
Strobilus plicosa	4.8	2.6	1.86	7	28	4.75	1.3	.8	2.65	.8
Tekoulina pricei	7.9	2.8	2.79	11	33	6.75	3.1	1.6	2.05	1.6
Achatinella lorata	15	9.5	1.58	5	120	4	1.1	1.25	1.65	1.3
Partula caledonica	21.8	12.5	1.75	5	168	3.75	1.3	.6	1.85	.6
Eua expansa	18	14	1.28	3	166	2.75	.7	.5	1.55	.2
Samoana conica	20	13.2	1.52	9999	167	3.25	1	.8	1.45	.9
Leptachatina balteata	10.4	4.9	2.13	6.5	75	4.75	1.1	1.25	2.4	1.1
Amastra pullata	19.5	12.9	1.51	5.25	150	4.25	1.2	1	2.05	1.1
Cochlicopa lubrica	7	2.4	2.93	6	35	4.5	1.5	1.25	1.75	.9
Pyramidula rupestris	1.6	2.4	.66	4	9	3.75	1.8	.7	2.25	.6
Bothriopupa breviconus	1.6	1.3	1.25	4.3	2	4	.9	.9	2.2	.6
Sterkia eyriesii	1.8	1.1	1.62	4.25	3	4	1.1	1.1	2.8	.8
Orcula dolium	7.3	3.5	2.09	8.5	40	5.7	2.5	1	2.2	.6
Pagodulina serveri	3.2	2	1.6	7.25	19	6	1.5	1.3	3.2	.6
Solatopupa similis	10.6	3.6	2.9	8.4	53	6.5	1.5	1.4	3.6	.7
Gyliotrachela depressispira	1.7	3.2	.53	3	13	3	.7	.5	1.8	.5
Pupilla muscorum	4	2	2	6.25	18	5.25	2.1	.9	2.25	.66
Lauria cylindracea	4.4	2.2	2	6.5	25	5.4	2.25	1.1	2.15	.6
Vallonia albula	1.3	2.7	.48	3.3	5	2	.8	.6	.6	.5
Ptychopatula dioscoricola	2	1.92	1.04	3	8	2.5	.75	.7	1.05	.5
Acanthinula aculeata	3.2	2.3	1.39	4.25	10	4.1	.7	1.4	2	1.1
Spermodea lamellata	1.7	2.2	.77	5.1	7	4.3	1	1	2.3	.75
Klemmia magnicosta	1.8	3.2	.56	5	24	3.75	.75	1	2	.8
Strobilops aenea	1.5	2.4	.62	5	6	3.75	.75	1.4	1.6	1.1
Chondrula tridens	10	4	2.5	6.8	55	5.8	1.4	1	3.4	1
Imparietula jousseaumei	10	4.6	2.17	6.3	67	6.2	1.75	1.3	3.15	1
Ena montana	14.8	8.5	1.74	7	83	6	1.3	1.1	3.6	1.1
Zebrina eburnea	25.1	7.8	3.22	9	89	7.5	1.9	1.3	4.3	1.25
Rachistia histrio	13	8.3	1.57	5.9	112	3.75	1	.75	2	1
Cerastua somaliensis	13.7	8.3	1.65	6.2	113	4.5	.75	1.25	2.5	1.5
Amimopima macleayi	12.5	8	1.56	5.5	82	9999	9999	9999	9999	9999
Draparnaudia michaudi	10	8.5	1.18	6.5	92	9999	9999	9999	9999	.9
Succinea putris	17.4	9.6	1.8	3	131	2.5	.3	.5	1.7	.6
Succinea propinqua	9	6.7	1.35	2	78	1.5	.25	.25	1	.5
Hyalimax perlucidus	8000	8000	8000	8000	128	8000	8000	8000	8000	8000
Omalonyx matheroni	8000	8000	8000	8000	152	8000	8000	8000	8000	8000
Aneitea simrothi	8000	8000	8000	8000	130	8000	8000	8000	8000	8000
Athoracophoridae sp.	8000	8000	8000	8000	127	8000	8000	8000	8000	8000
Thaumatodon hystricelloides	2.7	4	.67	5.5	26	3.65	.75	.8	2.1	.6
Libera fratercula	4.5	5.5	.82	7	49	5	.8	1.2	3	1.2
Trachycystis capensis	4.7	2.9	1.62	5.25	36	4.3	.6	1	2.7	1
Charopidae sp.	9999	3.9	9999	6	9999	3.25	.75	1.1	1.6	.9
Annoselix dolosa	3.3	5.7	.59	4.3	41	3.5	.75	.8	1.95	.7
Luinodiscus sp.	9999	9999	9999	9999	9999	9999	9999	9999	9999	.7
Pseudocharopa lidgbirdi	9999	9999	9999	9999	9999	9999	9999	9999	9999	9999
Mystivagor mastersi	6.9	4.7	1.47	3	51	9999	9999	9999	9999	.6
Ranfurlya constanceae	8000	8000	8000	8000	80	1	.15	.3	.35	9999
Pararhytida dictyodes	16	21	.76	6.2	192	3.7	.75	1.2	1.95	1
Pararhytida marteli	9.8	17.9	.55	5.9	141	5.5	.9	1.1	3.5	1

	H	D	H/D	WH	TA	LV	LP	ST	SS	LS
Pararhytida mouensis	12.6	21.5	.59	6.1	175	4.5	.9	1.1	2.5	1
Andrefrancia sp.	3.6	7.4	.49	4.5	45	2.75	.5	1	1.25	1
Stephanoda binneyana	6.5	14.5	.45	5	109	3.7	.6	.8	2.3	.6
Cystopelta purpurea	6000	6000	6000	6000	126	6000	6000	6000	6000	6000
Paralaoma lateumbilicata	.8	1.22	.66	3.1	1	3	.5	.7	1.7	.5
Phrixgnathus erigone	3.5	4.1	.86	5.5	32	3.7	.75	1	1.95	.8
Laoma leiomonas	2.9	2.1	1.38	7.5	17	4	.5	1.4	2.1	1.25
Discus rotundatus	2.7	5.5	.49	5.25	38	3.6	.6	.5	2.5	.5
Discus patulus	3.3	8	.41	5.25	43	9999	9999	9999	9999	.5
Anguispira alternata	13	23.9	.54	5	149	3.75	.75	.75	1.75	.9
Helicodiscus parallelus	1.8	4	.45	4	21	3.2	.6	.6	2	.5
Hemphillia camelus	6000	6000	6000	6000	114	6000	6000	6000	6000	6000
Ariolimax columbianus	8000	8000	8000	8000	226	8000	8000	8000	8000	8000
Aphallarion buttoni	8000	8000	8000	8000	225	8000	8000	8000	8000	8000
Zacoleus idahoensis	8000	8000	8000	8000	95	8000	8000	8000	8000	8000
Hesperarion niger	8000	8000	8000	8000	129	8000	8000	8000	8000	8000
Prophysaon humile	8000	8000	8000	8000	125	8000	8000	8000	8000	8000
Arion rufus	8000	8000	8000	8000	207	8000	8000	8000	8000	8000
Geomalacus maculosus	8000	8000	8000	8000	172	8000	8000	8000	8000	8000
Oopelta granulosa	8000	8000	8000	8000	196	8000	8000	8000	8000	8000
Oopelta nigropunctata	8000	8000	8000	8000	198	8000	8000	8000	8000	8000
Philomycus carolinianus	8000	8000	8000	8000	132	8000	8000	8000	8000	8000
Philomycus bilineatus	8000	8000	8000	8000	182	8000	8000	8000	8000	8000
Phenacolimax major	6000	6000	6000	6000	64	2.5	.2	.5	1.8	9999
Phenacolimax? ugandensis	6000	6000	6000	6000	97	1.5	.15	.35	1	9999
Plutonia atlantica	8000	8000	8000	8000	144	8000	8000	8000	8000	8000
Vitrea crystallina	1.4	3.1	.45	4.2	11	2.5	.5	.9	1.1	.6
Mesomphix inornatus	6	11.6	.52	4.25	84	4.5	.5	.7	3.3	.7
Aegopinella nitidula	3.5	7.1	.49	3.5	50	3	.4	.6	2	.6
Zonites algirus	22.4	38	.59	6.5	211	3.6	.6	1	2	1.3
Oxychilus draparnaudi	7	15	.47	6	106	2.25	.3	.8	1.15	.7
Daudebardia lederi	8000	8000	8000	8000	63	8000	8000	8000	8000	8000
Daudebardia sp.	8000	8000	8000	8000	96	8000	8000	8000	8000	8000
Ventridens acera	12	17.2	.7	7	151	5	.75	1.5	2.75	1.4
Zonitoides arboreus	1.8	3.4	.52	3.7	16	3.2	.75	.6	1.85	.6
Gastrodonta interna	4.7	7.1	.66	7.7	65	6	1.1	1.3	3.6	1.3
Parmacella valenciennesi	8000	8000	8000	8000	201	8000	8000	8000	8000	8000
Parmacella deshayesi	8000	8000	8000	8000	205	8000	8000	8000	8000	8000
Milax gagates	8000	8000	8000	8000	169	8000	8000	8000	8000	8000
Limax maximus	8000	8000	8000	8000	224	8000	8000	8000	8000	8000
Trochomorpha sp.	6.2	9.9	.62	5.8	79	5.3	.6	1.5	3.2	1.4
Conibycus cf. *dahli*	6.5	7.7	.84	4.1	56	3	.9	.9	1.2	.6
Discoconulus sp.A	5.4	6.8	.79	3.5	58	2.3	.25	.8	1.25	.8
Discoconulus sp.C	3.3	4	.825	5.2	31	3.5	.75	.75	2	.8
Coneuplecta sp.B	3.8	4.5	.84	5.1	39	2.2	.7	.7	.6	.5
Coneuplecta sp.D	5.9	6.3	.94	5.9	59	4.7	.9	1	2.8	.8
Coneuplecta sp.E	2.9	3.4	.85	5.9	23	4.6	.75	1.1	2.75	.9
Vitrinopsis sp.1	6000	6000	6000	6000	60	2.7	.3	.8	1.2	.75
Vitrinopsis sp.2	6000	6000	6000	6000	61	2.25	.25	.8	1.2	.75
Kalidos oleatus	23.5	36	.65	4.5	221	4	.5	1	2.5	1.1
Malagarion paenelimax	6000	6000	6000	6000	100	1.5	.25	.7	.5	9999
Helicarionidae sp.	4	6.6	.61	3.25	86	3	.35	.65	2	.6
Everettia corrugata	10	15.3	.65	4.4	123	4.25	.6	.9	2.75	1.2
Parmarion martensi	6000	6000	6000	6000	111	6000	6000	6000	6000	6000
Microparmarion pollonerai	6000	6000	6000	6000	122	6000	6000	6000	6000	6000
Hemiplecta humphreysiana	39	68	.57	4.9	233	3.25	.75	.5	2	.8
Mariaella dussumieri	8000	8000	8000	8000	176	8000	8000	8000	8000	8000
Trochozonites percarinatus	7.9	11.7	.675	7	107	3.25	1.1	1.1	1.05	1.1
Gymnarion sowerbyanus	6000	6000	6000	6000	206	2.5	.25	.5	1.75	9999
Acantharion browni	6000	6000	6000	6000	177	3	.25	.7	2.15	9999
Mesafricarion maculifer	6000	6000	6000	6000	115	2	.15	.3	1.55	9999

	H	D	H/D	WH	TA	LV	LP	ST	SS	LS
Trochonanina simulans	8.5	14	.6	4.6	124	3.2	.6	.8	1.8	.8
Granularion lamottei	6000	6000	6000	6000	170	2	.15	.25	1.6	9999
Estria sp.A	8000	8000	8000	8000	200	8000	8000	8000	8000	8000
Tresia parva	8000	8000	8000	8000	99	8000	8000	8000	8000	8000
Elisolimax madagascariensis	8000	8000	8000	8000	208	8000	8000	8000	8000	8000
Atoxon pallens	8000	8000	8000	8000	171	8000	8000	8000	8000	8000
Cecilioides acicula	4.6	1.3	3.54	5.3	14	5	.9	1	3.1	1
Subulina octona	21	4.3	4.88	9.5	54	5.25	1.2	1.8	2.25	1.7
Bocageia carpenteri	35	15.5	2.26	5.6	193	4.75	1	1	2.75	.9
Pseudoglessula hessei	11	5.6	1.96	6.2	74	5	1	1.25	3.75	1.25
Rumina decollata	25	10	2.5	4.5	148	5.25	2	1.25	3	1
Achatina fulica	71	41	1.73	7	228	4.5	1.2	.8	2.5	.7
Nenia tridens	24.3	5	4.86	7	93	5.25	2.5	1.5	1.25	1.3
Albinaria olivieri	18.2	4.2	4.36	12	76	7.5	2.5	1.5	3.5	1.25
Itala itala	13.8	2.6	5.3	10	52	4.75	1.5	1.1	3.15	1
Spiraxis futilis	3	.9	3.33	6.3	4	4.6	1.5	1.4	1.7	1.1
Varicella biplicata	4.6	1.3	3.54	5.3	15	5.5	.75	.3	4.45	.3
Poiretia dilatata	32	11.7	2.73	6	174	4	.4	.3	3.3	.3
Streptostyla streptostyla	20	9	2.2	9999	154	9999	9999	9999	9999	9999
Euglandina carminensis	48	19	2.53	9999	217	4.5	.4	1	3.1	1
Strebelia berendti	8000	8000	8000	8000	104	8000	8000	8000	8000	8000
Testacella europaea	8000	8000	8000	8000	202	8000	8000	8000	8000	8000
Trigonephrus rosaceus	24.6	26.8	.92	4.1	214	2.75	.7	.2	1.85	.5
Dorcasia alexandri	15.9	27.5	.58	4.1	194	3	.75	.5	1.75	.5
Strophocheilus chilensis	19.2	14.2	1.35	4	190	3	.7	.3	2	.5
Strophocheilus oblongus	9999	9999	9999	9999	236	9999	9999	9999	9999	9999
Pedinogyra sp.	24	60.5	.4	5.1	229	2.4	.7	.6	1.1	.6
Hedleyella falconeri	57	60	.95	3.9	235	3.75	.6	.75	2.4	.75
Pygmipanda kershawi	22	45	.49	5	218	4.66	.7	.8	3.16	.75
Anoglypta launcestonensis	19.5	33.5	.58	9999	203	9999	9999	9999	9999	9999
Caryodes sp.	24	14.6	1.64	4.5	160	3.5	.7	.6	2.2	.6
Pandofella whitei	6000	6000	6000	6000	183	1.5	.2	.3	1	9999
Macrocyclis laxata	35	73	.48	4.3	232	3	.7	.3	2	.3
Panda larreyi	17.7	35	.51	4	213	3.1	.5	.6	2	.6
Ampelita petiti	15.1	26.9	.56	5.25	180	3.3	.7	.3	2.3	.3
Helicophanta vesicalis	40	74	.54	3.5	234	3	.7	.3	2	.4
Clavator eximius	83	32	2.59	6	223	3.75	1	.6	2.15	.6
Stylodon studerianus	39.8	60.5	.66	5	231	4.6	1.5	.5	2.6	.8
Acavus superbus	47	57	.82	4.2	227	3	.7	.6	1.7	.9
Bostryx bermudezae	17.1	4.7	3.64	6.75	73	5.5	1.2	1.2	3.1	1.2
Cochlorina aurisleporis	33	21.5	1.53	5	179	3.5	1.1	.8	1.6	.7
Placostylus fibratus	84	38.5	2.18	6.7	230	3.15	.75	.9	1.5	.7
Discoleus azulensis	21.8	11	1.98	5	146	3.5	.75	.7	2.05	.7
Plagiodontes daedaleus	25.6	13	1.97	6.75	145	4.5	1.3	.7	2.5	.6
Anostoma depressa	15	31	.48	4.3	181	9999	9999	9999	9999	9999
Simpulopsis miersi	18.3	18	1.02	3.25	153	2.5	.6	.6	1.3	.65
Pellicula depressa	8000	8000	8000	8000	195	8000	8000	8000	8000	8000
Cerion copium	19.1	10.9	1.74	9.25	133	6	3	1.2	2.8	.9
Cerion casablancae	29	12.7	2.28	10.75	134	6.75	2.3	1.25	3.2	1.2
Berendtia taylori	47	14	3.36	10.5	165	9999	2	1.2	9999	1.1
Macroceramus signatus	14.7	6.9	2.13	10.2	105	5.3	1.3	1.7	2.3	1.6
Urocoptis procera	25	8	3.12	8	138	6.75	2.25	2.25	2.25	2
Systrophia eudiscus	4.2	10	.42	5.8	101	4.7	1	1	2.7	.9
Systrophia cayennensis	4.7	8.6	.55	4.25	71	0	.5	.65	9999	.6
Tamayoa decolorata	3.25	6.5	.5	4.2	48	0	.5	.6	9999	.6
Haplotrema concavum	9	21	.43	4.3	156	2.75	.35	.65	1.75	.5
Haplotrema minimum	9	19.5	.46	4.3	155	9999	9999	9999	9999	9999
Priodiscus serratus	3.3	6.5	.51	5.25	46	2	.4	.4	1.2	.3
Ouagapia raynali	9999	9999	9999	9999	9999	9999	9999	9999	9999	9999
Diplomphalus megei	5.1	7.8	.65	3.8	72	3.25	1	.3	1.95	.3

	H	D	H/D	WH	TA	LV	LP	ST	SS	LS
Rhytida inaequalis	12	24	.5	4.25	163	2	.5	.35	1.15	.3
Nata cf. *vernicosa*	6.2	11.1	.56	4.25	87	4.2	.5	.1	3.6	.3
Schizoglossa novoseelandica	8000	8000	8000	8000	140	8000	8000	8000	8000	8000
Chlamydephorus gibbonsi	8000	8000	8000	8000	212	8000	8000	8000	8000	8000
Edentulina sp.	33	15	2.2	6.15	188	5	1.25	.25	3.5	.4
Gonaxis enneoides	9999	9999	9999	9999	9999	9999	9999	9999	9999	9999
Ptychotrema sp.	14.7	7.2	2.04	7	110	6.8	2.1	.8	3.9	.6
Polygyra matermontana	4.6	8.5	.54	4.6	68	3.2	.75	.6	1.85	.9
Mesodon andrewsae	25.5	30.5	.84	5.7	210	5.5	1.5	.75	3.25	1.2
Trilobopsis trachypepla	4.8	7.9	.61	4.75	69	3.5	1.1	.9	1.5	.5
Triodopsis fraudulenta	7.1	14.3	.5	5.1	119	3.75	.75	.7	2.3	.6
Allogona ptychophora	14	19.3	.72	5.1	159	5	.9	.5	3.6	.5
Thysanophora horni	2.8	4.2	.66	3.7	29	2.2	.6	.55	1.05	.5
Lacteoluna turbiniformis	5.4	7.5	.72	5.4	66	4.2	.6	1	2.6	1
Proserpinula opalina	3	5.7	.53	4.15	37	3.75	.6	.9	2.25	.9
Sagda cf. *grandis*	22.1	23.7	.93	8.8	189	6.5	2.5	2	2	2.2
Corilla humberti	19.8	24.5	.81	5	187	1.75	.8	.65	.3	.65
Sculptaria collaris	2	6.4	.31	4.3	34	2.6	.9	.6	1.1	.6
Plectopylis sp.1	4.2	10.4	.4	6.1	77	3	1	.6	1.4	.5
Plectopylis sp.2	5.6	13.9	.4	7.25	94	5	.8	.9	3.3	.8
Craterodiscus pricei	2.1	5	.38	5.5	30	2.2	.9	.6	.7	.6
Pleurodonte lychnuchus	16	26.8	.6	4.5	191	3.75	1.1	.8	1.85	.7
Labyrinthus leprieurii	11.1	22.5	.49	4.75	158	4	1.1	1	1.9	1.1
Solaropsis undata	29	48	.6	5.5	222	4	2	1	2	1.1
Psadara nubeculata	8	13	.62	3.8	103	9999	9999	9999	9999	9999
Psadara marmatensis	6.4	10.4	.62	3.5	98	2.75	.6	.5	1.65	.5
Rhagada sp.	10	15.6	.64	4.8	135	3.25	.75	.8	1.7	.5
Sinumelon lennum	21.5	24	.9	4.75	197	3.2	.7	.6	1.75	.5
Amplir hagada burnerensis	13	18.7	.69	4.3	157	4	1	.66	2.34	.6
Amphidromus cognatus	22	16	1.37	9999	173	4	.5	.6	2.9	.65
Plectotropis goniocheila	5.6	9.7	.58	5	90	3.1	.8	.8	1.5	.8
Ammonitella yatesi	3.5	7.5	.47	6.3	44	4.25	1	.9	2.4	.6
Glyptostoma gabrielense	11.6	23.6	.49	5	185	3.25	.75	.75	1.75	.45
Oreohelix barbata	7	13.6	.51	4.25	102	2.5	.6	.6	1.3	.4
Helicostyla palawanensis	29	48	.6	5.5	219	4	1	.75	2.25	.8
Cochlostyla melanocheila	31.8	43.7	.73	4.1	220	9999	9999	9999	9999	9999
Bradybaena tourannensis	11.6	13	.89	4.9	137	5	.75	.65	3.6	.4
Averellia coactiliata	4.1	10.6	.39	4	91	3.25	.4	.75	2.1	.9
Leptarionta trigonostoma	19	24	.79	4.2	186	3	.45	.6	1.95	.8
Monadenia fidelis	18.9	31.3	.6	6.4	204	3.75	.95	.55	2.25	.75
Helminthoglypta sequoicola	19.8	29.9	.66	6.2	215	5.1	1.2	.5	3.4	.45
Epiphragmopora claromphalus	14.5	28	.52	4.1	199	3.2	.7	.5	2	.5
Sonorella walkeri	14	23	.61	4.3	162	3.3	.75	.5	2.05	.6
Cepolis varians	13.6	15.2	.89	4.75	139	4.2	1.2	1	2	1.2
Cepolis maynardi	7.5	12.7	.59	4.2	117	2.3	.45	.7	1.15	1.1
Sphincterochila zonata	17.8	22.4	.79	4.75	164	3.25	.7	.55	2	.5
Halolimnohelix sericata	10.4	15.2	.68	5.1	142	3.5	.55	.7	2.25	.7
Candidula unifasciata	5.2	7	.74	4.1	62	2.9	.5	.6	1.8	.6
Candidula intersecta	3.7	6	.62	3.8	42	3.25	75	.75	1.75	.75
Cernuella virgata	10.5	14.4	.73	5.3	147	3.5	.66	.7	2.2	.7
Leucochroa explanata	5.2	12.4	.42	4.5	108	2.75	.6	.4	1.75	9999
Helicella itala	7.2	13.8	.52	5.25	118	3.65	.55	.8	2.3	.6
Trochoidea elegans	6	9.5	.63	6.3	88	4.25	1	.7	2.55	9999
Trochoidea geyeri	4	6.3	.63	4.3	47	2.7	.7	.6	1.4	9999
Helicopsis striata	5.7	7.2	.79	4.5	70	3.1	.9	.6	1.6	.45
Helicopsis sp.	9999	9999	9999	9999	9999	2	.5	.55	.95	.3
Helicopsis apicina	4.6	7	.66	4.25	57	3	.5	.6	1.9	.35
Cochlicella acuta	14.2	5.3	2.68	9.1	81	7	1.25	1.7	4.05	1.25
Monacha cartusiana	8.9	14.2	.63	6	143	5.4	.75	1	3.65	.7

	H	D	H/D	WH	TA	LV	LP	ST	SS	LS
Hygromia limbata	11	16	.69	6	136	4	.9	.75	2.35	.75
Trichia hispida	5.8	8.6	.67	5.1	85	3.4	.9	.6	1.9	9999
Helicodonta obvoluta	5.6	11.6	.48	6	116	4.25	.8	.9	2.55	.8
Elona quimperiana	13	26.2	.5	4.5	209	3.4	.7	.55	2.15	.5
Arianta arbustorum	17	20	.85	5.25	178	3.5	1	.65	1.85	.5
Helicigona lapicida	7.4	15.5	.48	4.3	121	2.5	.9	.5	1.1	.4
Theba pisana	14.1	19.1	.74	5	161	2.9	.7	.6	1.6	9999
Cepaea nemoralis	18.4	24	.77	4.75	184	4.3	.8	.6	2.9	.8
Helix aspersa	32.7	37.6	.87	4	216	3.6	.75	.6	2.25	9999

APPENDIX C. UPPER LIMITS OF CLASSES USED IN FACTOR ANALYSES

The size of each class is in parentheses.

TEXT-FIGURES 5, 6, 7 (PROPORTIONS OF VISCERAL MASS, APPENDIX B)

HD1	HD2	HD3	HD4	HD5	TA1	TA2	TA3	TA4	TA5
0.52(32)	.66(37)	.89(28)	1.96(31)	5.3(31)	35(32)	77(32)	134(32)	184(32)	235(31)
WH1	WH2	WH3	WH4	WH5	LP1	LP2	LP3	LP4	LP5
4.25(39)	4.9(25)	5.3(32)	6.3(32)	12(31)	.6(39)	.75(40)	.9(18)	1.25(33)	3.1(29)
LS1	LS2	LS3	LS4	LS5	SS1	SS2	SS3	SS4	SS5
0.5(38)	.6(28)	.8(34)	1.1(34)	3.8(25)	1.6(32)	2(43)	2.25(21)	2.8(32)	4.45(31)
ST1	ST2	ST3	ST4	ST5					
0.6(51)	.7(17)	.9(18)	1.2(34)	2(26)					

TEXT-FIGURES 10, 11, 12 (PULMONARY COMPLEX, APPENDIX B AND FIGS. 1–704)

HD1	HD2	HD3	HD4	HD5	TA1	TA2	TA3	TA4
0.55(37)	.75(40)	1(23)	2(29)	5.3(27)	46(39)	107(39)	164(39)	235(39)
LR1	LR2	LR3	LR4	UR1	UR2	UR3	UR4	LI1
0.33(43)	.45(37)	.63(39)	.99(39)	0(43)	2(17)	4(27)	5(69)	1(88)
LI2	LI3	LI4	RR1	RR2	RR3	CA1	CA2	RP1
2(26)	3(33)	4(9)	1(78)	2(52)	3(26)	0(107)	1(49)	.18(41)
RP2	RP3	RP4						
0.23(47)	.28(32)	.5(36)						

TEXT-FIGURES 13, 14, 15 (DIGESTIVE TRACT, APPENDIX B AND FIGS. 1–704)

HD1	HD2	HD3	HD4	HD5	TA1	TA2	TA3	TA4	TA5
0.52(32)	.66(37)	.89(28)	1.96(31)	5.3(31)	35(32)	77(32)	134(32)	184(32)	235(31)
BM1	BM2	OC1	OC2	OC3	OC4	SC1	SC2	SC3	SC4
1(149)	2(10)	0(103)	1(31)	2(5)	3(22)	1(14)	2(80)	3(43)	4(22)
IL1	IL2	IL3	IL4	PS1	PS2	PS3			
1(35)	2(59)	3(59)	4(6)	1(35)	2(107)	3(17)			

TEXT-FIGURES 16, 17, 18 (NERVOUS SYSTEM, APPENDIX B AND FIGS. 1–704)

HD1	HD2	HD3	HD4	HD5	TA1	TA2	TA3	TA4
0.6(45)	1.5(46)	8(45)	semislugs	slugs	55(39)	115(39)	169(39)	235(39)
CC1	CC2	CC3	CPD1	CPD2	CPD3	CPR1	CPR2	CPR3
1(12)	2(25)	3(119)	1(38)	2(81)	3(37)	.9(20)	1.2(86)	2.5(50)
PLD1	PLD2	PLD3	PLG1	PLG2	PLG3	VG1	VG2	VG3
2(39)	3(5)	1(137)	2(15)	3(4)	1(51)	2(71)	3(34)	1(112)
PAD1	PAD2	PAG1	PAG2	PAG3	PAG4	FG1	FG2	FG3
1(53)	2(103)	1(26)	2(13)	3(31)	4(86)	1(52)	2(53)	3(35)
FG4								
4(16)								

APPENDIX D. LIMITS OF CLASSES USED IN PHENETIC AND PHYLOGENETIC ANALYSES (CHARACTER STATES)

(TEXT-FIGURES 19–29, APPENDICES E,F,G)

The character states retained for phylogenetic reconstructions are denoted from 1 to n or from 1 to n′, from plesiomorphic to apomorphic. The data set is extracted from Appendix C and from the data set used in previous factor analyses. Some of the data missing from the latter have been found and added at this step to avoid the absence of some families (Appendix E).

GENERAL MORPHOLOGY									
HD1	HD2	HD3	HD4	HD5	HD6	HD7	HD8		
0.55	0.75	1.2	2	10	semislugs	slugs	missing		
WH1	WH2	WH3	WH4	WH5	WH6	WH7	WH8	WH9	
4.1	4.5	5	5.5	6.4	20	semislugs	slugs	missing	
TA1	TA2	TA3	TA4	TA5					
48	96	144	192	243					
LV1	LV2	LV3	LV4	LV5	LV6	LV7	LV8		
2.9	3.3	3.9	4.8	20	semislugs	slugs	missing		
LS1	LS2	LS3	LS4	LS5	LS6	LS7			
0.6	0.8	1.2	10	semislugs	slugs	missing			
SS1	SS2	SS3	SS4	SS5	SS6	SS7			
1.65	2	2.5	10	semislugs	slugs	missing			
ST1	ST2	ST3	ST4	ST5	ST6	ST7			
0.55	0.75	1.1	5	semislugs	slugs	missing			
PULMONARY COMPLEX									
LP1	LP2	LP3	LP4	LP5	LP6	LP7			
0.6	0.75	1.2	10	semislugs	slugs	missing			
LR1	LR2	LR2′	LR3	LR4	LR5	LR6			
0.45,0.7	0.36,0.45	0.7,1	0.25,0.36	0,0.25	semislugs, slugs	missing			
UR1	UR2	UR3	UR4						
0	2	4	5						
LI1	LI2	LI3	LI4	RR1	RR2	CA1	CA2		
1	2	3	4	1,2	0,1	0	1		
DIGESTIVE TRACT									
BM1	BM2	OC1	OC2	OC3	OC4				
1	2	0	1	2	3				
SC1	SC2	SC2′	SC3	PS1	PS2	PS2′			
1,2	2,3	1	3,4	1,2	2,3	1			
IL1	IL2	IL2′	IL4						
1,2	2,3	0,1	3,4						
NERVOUS SYSTEM									
CC1	CC2	CC3	CPD1	CPD2	CPD3	CPR1	CPR2	CPR3	CPR4
1	2	3	1	2	3	0.9	1.1	1.5	5
PLD1	PLD2	PLD3	PLG1	PLG2	PLG3	VG1	VG2	VG3	
1	2	3	1	2	3	1	2	3	
PAD1	PAD2	PAG1	PAG2	PAG3	PAG4	FG1	FG2	FG2′	FG3
1	2	1	2	3	4	1	2	3	4

APPENDIX E. CHARACTER STATES USED IN PHYLOGENETIC RECONSTRUCTIONS This data set is extracted from Appendices C and D, and from the data set used in previous factor analyses. Some of the data missing in the latter have been found and added at this step to avoid the absence absence of some families. Each line represents a species, in the same order as in Appendix A. The numbers preceding each generic name are those of the families or subfamilies, as in Appendix A.

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
01AURICULELLA	1	1	1	1	1	2′	1	1	3	3	4	2	2	1	1	2	2
01ELASMIAS	1	1	1	1	1	2′	1	1	2	3	4	0	0	1	1	1	2
01LAMELLIDEA	1	1	1	1	1	2′	1	1	2	2	4	2	1	1	2	1	2
01TORNATELLINA	1	1	1	1	1	2′	1	1	3	3	2	2	1	1	1	1	2
01STROBILUS	1	1	1	1	1	2′	1	1	3	3	4	2	1	1	1	1	2
01TEKOULINA	1	1	1	1	1	2′	1	1	3	1	2	2	2	1	1	1	2
02ACHATINELLA	1	1	1	1	1	2′	1	1	3	3	4	2	1	1	1	1	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
03PARTULA	1	1	2	1	1	2′	1	1	2	2	2	1	1	2	2	3	2
03EUA	1	3	0	2′	1	—	1	1	2	2	4	1	1	2	1	4	2
03SAMOANA	1	1	2	1	1	—	1	1	3	3	3	1	1	2	2	4	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
04LEPTACHATINA	1	1	1	1	1	2′	1	1	2	2	3	1	1	1	2	3	2
04AMASTRA	1	1	1	1	1	2′	1	1	2	2	4	1	1	3	1	4	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
05COCHLICOPA	1	1	1	1	1	2′	1	1	1	2	3	1	1	1	1	2	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
06PYRAMIDULA	1	1	2	1	1	2′	1	1	3	1	2	2	2	1	1	1	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
07BOTHRIOPUPA	1	1	1	1	1	—	1	1	3	2	3	2	2	1	1	2	2
07STERKIA	1	1	1	1	1	2′	1	1	—	—	—	—	—	—	—	—	—
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
08ORCULA	1	1	2	1	1	2′	1	1	3	2	3	1	1	2	1	3	2
08PAGODULINA	1	2	1	1	1	1	1	1	3	2	3	2	2	2	1	3	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
09SOLATOPUPA	1	1	2	2′	1	2′	1	1	2	2	1	1	1	2	1	1	2
09GYLIOTRACHELA	1	1	2	2′	1	2′	1	1	1	2	3	2	2	2	1	1	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
10PUPILLA	1	1	2	1	2	2′	1	1	3	1	2	2	2	2	1	2	2
10LAURIA	1	1	2	1	1	2′	1	1	2	2	2	2	2	2	1	2	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
11VALLONIA	1	1	2	1	2	2′	1	1	3	2	2	2	1	1	1	1	2
11PTYCHOPATULA	1	1	2′	1	2	2′	1	1	3	3	3	2	1	1	1	4	2
11ACANTHINULA	1	1	1	1	1	2′	2	1	2	3	2	2	1	1	2	4	2
11SPERMODEA	1	1	1	1	2	2′	1	1	3	2	1	2	1	1	1	3	3
11KLEMMIA	1	1	1	1	2	2′	1	1	3	2	2	2	1	1	1	1	2
11STROBILOPS	1	1	1	1	2	2′	1	1	3	2	3	2	2	1	2	2	1
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
13CHONDRULA	1	1	2	2′	1	2′	1	1	2	2	2	2	1	2	2	4	1
13IMPARIETULA	1	1	1	1	1	2′	1	1	2	3	3	1	1	2	1	4	2
13ENA	1	1	1	1	2	2′	1	1	2	3	2	2	1	1	2	4	1
13ZEBRINA	1	1	2	1	1	2′	1	1	3	2	2	1	1	2	1	4	2
13RACHISTIA	1	2	1	1	2	2′	2	1	3	3	2	1	1	2	2	4	2
13CERASTUA	1	1	1	1	1	2′	1	1	3	3	2	1	1	2	2	4	3
13AMIMOPIMA	1	1	1	2	2	2′	2	1	3	3	2	1	1	2	2	4	1
13DRAPARNAUDIA	1	1	1	2	2	2′	1	1	3	3	2	1	1	2	2	4	2
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
14SUCCINEA	1	1	1	1	1	3	4	2	2	3	1	1	1	2	2	4	3
14SUCCINEA2	1	1	1	2	1	3	4	2	—	—	—	—	—	—	—	—	—
14OMALONYX	1	1	2′	2	2	2	4	2	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
15ATHORACOPHORID	1	1	1	2	2′	—	4	—	3	3	2	0	0	1	2	4	3

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
16THAUMATODON	1	1	3	2	2	—	2	1	2	2	1	2	2	1	1	1	2
16LIBERA	1	1	3	2	2	3	2	1	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
17TRACHYCYSTIS	1	1	3	1	2	2	4	1	3	2	3	2	1	1	1	1	2
17RANFURLYA	1	1	3	2	2	—	4	2	3	3	1	1	1	1	2	1	1
17ANNOSELIX	1	1	3	1	2	3	4	1	3	2	1	2	1	1	1	1	2
17STEPHANODA	1	1	2′	1	2	2	4	1	2	2	1	2	1	1	1	1	2
17CHAROPID	1	1	3	2	2	3	2	1	3	2	3	2	1	1	1	1	1
17ANDREFRANCIA	1	1	3	1	2	—	4	1	3	2	2	2	1	1	1	1	1
17MYSTIVAGOR	1	1	3	2	2	2	4	1	3	2	2	2	1	1	1	2	2
17PARARHYTIDA1	1	1	3	1	2	3	4	2	—	—	—	—	—	—	—	—	—
17PARARHYTIDA2	1	1	3	1	2	4	4	2	—	—	—	—	—	—	—	—	—
17PARARHYTIDA3	1	1	3	1	2	3	4	2	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
18CYSTOPELTA	1	1	1	1	2	—	4	1	3	3	1	0	0	1	2	4	3
18PHRIXGNATHUS	1	1	3	1	2	3	4	1	3	2	3	2	1	1	2	1	2
18LAOMA	1	1	3	1	2	—	4	1	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
19ANGUISPIRA	1	1	2′	1	1	3	4	2	3	1	1	1	1	1	2	1	2
19DISCUS1	1	1	2′	1	2	3	4	2	—	—	—	—	—	—	—	—	—
19DISCUS2	1	1	1	1	2	3	4	1	—	—	—	—	—	—	—	—	—
19HELICODISCUS	1	1	1	1	2	2	4	2	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
20HEMPHILLIA	1	1	3	2	2	—	4	2	2	3	2	1	1	1	2	3	3
20OOPELTA	1	1	1	1	1	—	4	2	1	2	1	1	1	1	2	3	2′
20ARIOLIMAX	1	1	2′	1	2′	—	4	2	—	—	—	—	—	—	—	—	—
20APHALLARION	1	1	1	1	2′	—	4	2	—	—	—	—	—	—	—	—	—
20ZACOLEUS	1	1	—	—	—	—	4	2	—	—	—	—	—	—	—	—	—
20HESPERARION	1	1	3	1	2′	—	4	2	—	—	—	—	—	—	—	—	—
20PROPHYSAON	1	1	2	1	1	—	4	2	—	—	—	—	—	—	—	—	—
20ARION	1	1	2′	1	2′	—	4	2	—	—	—	—	—	—	—	—	—
20GEOMALACUS	1	1	1	1	2′	—	4	2	—	—	—	—	—	—	—	—	—
20OOPELTA2	1	1	1	1	1	—	4	2	—	—	—	—	—	—	—	—	—
21PHILOMYCUS1	1	1	3	1	1	—	4	2	3	3	2	0	0	2	2	3	3
21PHILOMYCUS2	1	1	1	1	2′	—	4	2	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
23PHENACOLIMAX1	1	1	2′	1	2	—	4	2	3	3	3	1	1	2	2	4	2
23PLUTONIA	2	1	2	2	2	—	4	2	3	2	3	1	1	3	2	3	2′
23PHENACOLIMAX2	1	1	1	1	2	—	4	2	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
24MESOMPHIX	1	1	2	2′	2	2	4	2	3	1	1	1	1	2	1	2	2
24AEGOPINELLA	1	1	2′	1	2	1	4	1	3	1	2	1	1	1	1	2	2
24ZONITES	1	1	2′	1	2	1	4	2	3	1	2	1	1	2	2	4	1
24OXYCHILUS	2	1	1	1	2	1	4	1	3	1	3	1	1	2	1	2	2
24VENTRIDENS	1	1	1	1	1	2	4	1	3	1	3	1	1	1	2	1	1
24GASTRODONTA	1	1	1	1	3	3	4	1	3	2	4	2	1	2	1	1	1
24VITREA	1	1	3	2	2	1	4	1	—	—	—	—	—	—	—	—	—
24DAUDEBARDIA	2	1	2	2	2	—	—	—	1	1	1	1	1	2	1	2	2
24ZONITOIDES	1	1	2	2	2	3	4	1	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
25PARMACELLA	1	1	1	2	2	—	4	2	1	1	2	1	1	2	2	4	1
25PARMACELLA2	1	1	1	2	2	—	4	2	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
26MILAX	1	1	2	2	2′	—	4	2	3	2	1	1	1	3	2	4	2′

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
27LIMAX	1	1	2′	1	2′	—	4	2	3	2	2	1	1	2	2	4	1

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
29TROCHOMORPHA	1	1	2′	1	2	2	4	1	3	3	2	2	2	2	2	2	1

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
30DISCOCONULUS1	1	1	3	1	2	1	4	1	3	3	2	2	1	1	2	1	2
30DISCOCONULUS2	1	1	3	2	2	3	4	1	3	2	1	2	2	1	2	1	2
30CONIBYCUS	1	1	3	2	2	—	—	—	—	—	—	—	—	—	—	—	—
30CONEUPLECTA1	1	1	3	2	3	3	4	1	—	—	—	—	—	—	—	—	—
30CONEUPLECTA2	1	1	1	1	3	3	4	1	—	—	—	—	—	—	—	—	—
30CONEUPLECTA3	1	1	3	2	2	2	4	1	—	—	—	—	—	—	—	—	—
30VITRINOPSIS	1	1	1	1	2	2′	4	1	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
31HEMIPLECTA	1	1	1	1	2	2′	4	1	3	3	2	1	1	2	2	3	1
31EVERETTIA	1	1	1	1	1	1	4	2	3	2	2	1	1	3	2	3	1
31MICROPARMARION	1	3	0	1	2	2′	4	2	3	3	3	0	1	1	2	4	3
31TROCHOZONITES	1	1	1	1	2	2	4	1	3	3	3	1	1	1	2	3	1
31ACANTHARION	1	3	3	1	1	2′	4	1	3	2	2	1	1	1	2	4	2
31TROCHONANINA	1	1	1	1	2	1	4	1	2	2	1	1	1	2	2	4	1
31ATOXON	1	4	0	2	2′	—	4	2	3	3	2	1	1	2	2	4	1
31KALIDOS	1	1	2′	1	1	1	4	1	—	—	—	—	—	—	—	—	—
31MARIAELLA	1	3	2	2	2	2′	4	2	—	—	—	—	—	—	—	—	—
31PARMARION	1	3	0	1	2	—	4	2	—	—	—	—	—	—	—	—	—
31HELICARION	1	3	2′	1	1	—	4	1	3	2	3	1	1	1	2	4	2
31GYMNARION	1	3	3	1	1	2′	4	1	—	—	—	—	—	—	—	—	—
31MESAFRICARION	1	3	3	1	1	—	—	—	3	2	2	1	1	2	2	4	1
31GRANULARION	1	4	0	2	2	—	—	—	2	3	2	2	2	2	2	4	1
31ELISOLIMAX	1	4	0	2	2′	2′	4	2	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
32CECILIOIDES	1	1	2	2′	2	4	4	2	3	2	2	1	1	2	1	3	1

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
33BOCAGEIA	1	1	2′	2′	2	1	4	2	3	2	4	1	1	1	2	4	2
33PSEUDOGLESSULA	1	1	2	2′	2	1	4	1	3	2	3	1	1	2	2	4	2
33RUMINA	1	2	2	2′	1	3	4	1	3	1	3	1	1	2	1	3	1
33SUBULINA	1	1	2	2′	2	2	4	1	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
34ACHATINA	1	3	2	2′	1	1	4	2	3	2	3	1	1	2	2	4	1

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
37NENIA	1	1	2	2′	2	3	1	2	1	2	3	1	1	2	1	3	1
37ALBINARIA	1	1	2	2′	2	3	1	2	1	2	2	2	1	1	1	4	1
37ITALA	1	1	2	2′	2	4	1	2	1	3	4	1	1	1	2	4	1

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
38VARICELLA	2	1	1	2	1	1	4	2	3	3	4	1	1	3	2	4	2
38POIRETIA	2	1	1	1	1	4	4	2	3	1	3	1	1	3	1	3	2
38STREBELIA	2	1	3	2	3	—	4	2	3	2	2	1	1	3	2	4	1
38SPIRAXIS	2	1	1	1	3	4	3	2	—	—	—	—	—	—	—	—	—

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
40TRIGONEPHRUS	1	1	2	2′	2′	1	1	2	3	1	3	1	1	1	2	4	1
40DORCASIA	1	3	2	2′	2′	2	1	2	3	1	3	1	1	1	1	4	1
40STROPHOCHEILUS	1	2	1	1	2′	1	1	1	2	1	3	1	1	2	2	4	1
40PEDINOGYRA	1	2	1	1	2′	4	2	2	2	1	2	1	1	1	2	4	1
40HEDLEYELLA	1	2	2	2′	2′	2	2	2	3	1	2	1	1	3	2	4	1
40PYGMIPANDA	1	2	2	1	2′	1	2	2	3	2	2	1	1	2	2	4	1
40CARYODES	1	1	2	2′	2′	1	2	2	3	1	3	1	1	2	1	3	1
40PANDOFELLA	1	3	0	1	1	2′	3	2	3	1	2	1	1	2	2	4	1
40PANDA	1	1	2	2′	2′	1	2	2	3	1	2	1	1	2	2	4	1
40AMPELITA	1	2	2	2′	2′	2	2	1	3	2	4	1	1	2	2	4	1
40HELICOPHANTA	1	2	2	2′	2′	1	2	2	3	1	3	1	1	2	2	4	2
40CLAVATOR	1	2	2′	2′	2′	3	1	1	3	1	3	1	1	1	2	4	2
40STYLODON	1	2	1	2′	2′	1	1	1	3	2	2	1	1	3	2	4	1
40ACAVUS	1	4	2	2′	2′	3	3	2	3	3	2	1	1	2	2	4	3
40ANOGLYPTA	1	2	2	1	2′	—	—	2	3	3	4	1	1	3	1	4	1

40MACROCYCLIS	2	2	2′	1	2′	—	2	2	3	1	2	1	1	2	2	4	1
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
41BOSTRYX	1	2	1	2	1	3	3	2	2	2	2	1	1	3	2	4	2′
41DISCOLEUS	1	3	1	2′	1	3	3	2	1	2	4	1	1	3	2	3	2′
41COCHLORINA	1	3	2	1	2′	3	3	2	—	—	—	—	—	—	—	—	—
41PLACOSTYLUS	1	3	2	1	1	3	4	2	—	—	—	—	—	—	—	—	—
41PLAGIODONTES	1	2	2	2′	2′	2	3	2	3	2	4	1	1	3	2	4	2′
41SIMPULOPSIS	1	3	2	1	2′	2	4	2	3	1	2	1	1	3	2	4	3
41PELLICULA	1	3	1	2	2′	2′	4	2	3	2	4	1	1	3	2	4	2′
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
43CERION1	1	1	1	1	1	4	1	2	2	2	3	1	1	2	1	3	1
43CERION2	1	1	1	2′	1	2	1	2	—	—	—	—	—	—	—	—	—
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
44BERENDTIA	1	1	2	2	—	3	3	2	3	1	2	1	1	2	2	4	2′
44MACROCERAMUS	1	1	2	2′	2	3	1	2	—	—	—	—	—	—	—	—	—
44UROCOPTIS	—	—	—	—	—	4	2	2	3	1	2	1	1	2	2	3	2′
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
45SYSTROPHIA1	1	1	3	1	2	3	2	1	3	2	2	2	2	1	2	1	2
45SYSTROPHIA2	1	1	3	2	2	1	4	—	—	—	—	—	—	—	—	—	—
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
46HAPLOTREMA1	1	1	1	1	2	2	4	1	—	—	—	—	—	—	—	—	—
46HAPLOTREMA2	—	—	—	—	—	—	—	—	3	2	3	1	1	2	2	3	2′
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
47PRIODISCUS	2	1	1	1	3	3	4	2	3	2	2	1	1	3	1	3	3
47DIPLOMPHALUS	2	1	1	2	2′	3	2	2	3	3	2	1	1	2	1	3	3
47NATA	2	2	3	2	2′	1	2	2	3	1	2	1	1	2	1	3	1
47RHYTIDA	2	1	3	2	2′	2	2	2	—	—	—	—	—	—	—	—	—
47SCHIZOGLOSSA	2	2	0	2	2	1	4	2	—	—	—	—	—	—	—	—	—
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
49PTYCHOTREMA	2	1	2	2	2	4	4	2	3	2	2	1	1	2	1	3	1
49EDENTULINA	2	3	2	1	2′	4	4	2	—	—	—	—	—	—	—	—	—
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
50POLYGYRA	1	1	2′	1	2	1	4	1	3	3	3	1	1	2	2	4	2′
50MESODON	1	3	1	1	2′	1	4	1	3	1	3	1	1	2	2	4	2′
50TRIODOPSIS	1	2	2	2′	2	2	4	1	3	2	3	1	1	3	2	4	2′
50TRILOBOPSIS	1	2	1	1	2	3	4	1	—	—	—	—	—	—	—	—	—
50ALLOGONA	1	3	2	2′	2	1	4	1	—	—	—	—	—	—	—	—	—
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
51PROSERPINULA	1	1	3	1	2	1	4	2	3	2	2	1	1	3	2	4	2′
51SAGDA	1	1	2	1	2′	4	4	2	3	2	2	1	1	2	2	4	2′
51LACTEOLUNA	1	1	3	1	2	1	4	2	—	—	—	—	—	—	—	—	—
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
52CORILLA	1	1	1	2′	2′	3	1	2	2	2	2	1	1	2	2	4	1
52SCULPTARIA	1	1	3	2	2′	4	1	2	3	2	2	2	1	3	1	1	1
52PLECTOPYLIS	1	2	1	1	2′	4	1	2	1	1	2	2	1	3	1	1	1
52CRATERODISCUS	1	1	3	2	3	4	4	2	3	2	2	2	1	3	1	4	3
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
53PLEURODONTE	1	2	1	1	2′	2	4	2	3	2	3	1	1	2	2	4	3
53LABYRINTHUS	1	2	1	1	1	1	4	2	3	2	4	1	1	1	2	3	2′
53AMPLIRHAGADA	1	4	1	1	1	1	4	1	3	2	3	1	1	2	2	4	1
53PLECTOTROPIS	1	2	1	1	2	1	4	1	3	2	1	1	1	3	2	4	2′
53SOLAROPSIS	1	2	1	1	2′	1	3	2	—	—	—	—	—	—	—	—	—
53RHAGADA	1	3	1	1	2′	1	4	1	—	—	—	—	—	—	—	—	—
53SINUMELON	1	2	2′	1	1	2	4	1	—	—	—	—	—	—	—	—	—
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
54AMMONITELLA	1	1	1	1	1	4	2	2	1	1	1	2	2	1	2	3	2
54GLYPTOSTOMA	1	1	2	2′	1	2	2	2	3	1	2	1	1	1	1	3	1
55OREOHELIX	1	1	1	1	2′	2	2	2	1	3	3	2	1	1	2	3	1
	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG

56HELICOSTYLUS	1	3	2	2′	1	2′	4	1	3	1	2	1	1	3	2	4	3
56BRADYBAENA	1	4	1	1	1	1	4	1	3	2	2	1	1	2	2	4	1

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
57THYSANOPHORA	1	1	1	1	2	1	3	1	3	2	2	1	1	3	2	4	2′
57AVERELLIA	1	2	1	1	1	1	3	1	3	3	2	1	1	2	2	4	2′
57HELMINTHOGLYPTA	1	4	1	1	2′	2	3	2	3	1	1	1	1	2	2	4	2′
57EPIPHRAGMOPORA	1	2	1	1	2′	1	4	2	3	1	3	1	1	3	2	4	2′
57SONORELLA	1	3	1	2′	2′	1	3	2	3	3	2	1	1	2	2	4	2′
57CEPOLIS1	1	2	1	2′	1	1	4	1	3	2	3	1	1	2	2	4	2′
57MONADENIA	1	3	1	1	1	1	3	1	—	—	—	—	—	—	—	—	—
57CEPOLIS2	1	3	1	1	1	2′	4	1	—	—	—	—	—	—	—	—	—
57PSADARA	1	2	2′	1	1	2′	4	1	3	2	3	1	1	2	2	4	1

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
58SPHINCTEROCHILA	1	1	3	1	2′	2	4	2	3	1	3	1	1	2	1	3	1
58HALOLIMNOHELIX	1	3	2′	1	1	1	3	2	3	2	1	1	1	2	2	4	2′
58CANDIDULA	1	1	1	1	1	1	3	2	3	2	2	1	1	2	2	4	2′
58HELICELLA	1	2	1	1	1	3	3	2	3	2	3	1	1	3	2	4	2′
58COCHLICELLA	1	2	1	1	2	3	3	2	3	2	3	1	1	2	2	4	2′
58MONACHA	1	1	1	1	2	1	3	2	3	2	2	1	1	3	2	4	2′
58HELICODONTA	1	1	1	1	2	3	3	2	3	2	3	1	1	2	2	4	1
58HELICOGONA	1	2	1	1	2	2	3	2	3	2	3	1	1	2	2	4	1
58CERNUELLA	1	2	1	1	1	2	3	2	—	—	—	—	—	—	—	—	—
58TROCHOIDEA	1	1	1	1	1	3	3	2	—	—	—	—	—	—	—	—	—
58HELICOPSIS1	1	2	1	1	2	2	3	2	—	—	—	—	—	—	—	—	—
58HELICOPSIS2	1	2	1	1	2	1	3	2	3	3	3	1	1	2	2	4	2′
58HELICOPSIS3	1	1	2	2′	2	1	3	2	—	—	—	—	—	—	—	—	—
58HYGROMIA	1	3	1	1	1	2	3	2	—	—	—	—	—	—	—	—	—
58ELONA	1	4	1	1	1	2	4	2	—	—	—	—	—	—	—	—	—
58ARIANTA	1	3	1	1	1	3	3	2	—	—	—	—	—	—	—	—	—
58THEBA	1	4	1	1	1	2	3	2	—	—	—	—	—	—	—	—	—
58HELIX	1	3	1	1	2′	3	4	2	1	1	1	2	2	1	2	3	2
58CEPAEA	1	3	1	1	2′	2	3	2	3	2	1	1	1	3	2	4	2′

APPENDIX F. CHARACTER STATES OF CCAs OF STYLOMMATOPHORAN FAMILIES (NODES IN TEXT—FIGS. 20–22)

The character states of the families correspond to the lowest values in each familial group in Appendix E. For the Orthurethra, the symplesiomorphies and synapomorphies of all members of the group, and the autapomorphies of one member only have been eliminated: the former contribute no information at all, and the latter modify the distances without contributing any information about relationships. For taxa not belonging to the Orthurethra, the columns that have been doubled (SC, PS, IL, FG) correspond to characters of which the plesiomorphic state is in the middle of the morphocline, denoted either from 1 to n or from 1 to n′ in Appendix E. The numbers on the left, denoted "=n=" correspond to the hypothetical nodes in Text—Figs. 20–22 (constructed by the algorithm).

ORTHURETHRA (Text–Fig. 20)	SC	PS	CC	CPD	CPR	PLD	PLG	VG	PAG	FG
01ACHATINELLIDAE	1	1	2	1	2	2	1	1	1	2
03PARTULIDAE	2	1	2	2	2	1	1	2	3	2
04AMASTRIDAE	1	1	2	2	3	1	1	1	3	2
05COCHLICOPIDAE	1	1	1	2	3	1	1	1	2	2
06PYRAMYDULIDAE	2	1	3	1	2	2	2	1	1	2
07VERTIGINIDAE	1	1	3	2	3	2	2	1	2	2
08ORCULIDAE	1	1	3	2	3	1	1	2	3	2
09CHONDRINIDAE	2	2	1	2	1	1	1	2	1	2
10PUPILLIDAE	2	1	2	1	2	2	2	2	2	2
11VALLONIIDAE	1	1	2	2	1	2	1	1	1	1
13ENIDAE	1	1	2	2	2	1	1	1	4	1
=1=	1	1	3	2	3	1	1	1	2	2
=2=	1	1	2	2	2	1	1	1	3	2
=3=	2	1	2	1	2	2	2	1	1	2
=4=	1	1	2	2	2	1	1	1	3	1
=5=	1	1	1	2	2	1	1	1	2	1
=6=	1	1	1	2	1	1	1	1	1	1
=7=	1	1	2	1	1	2	1	1	1	1
=8=	1	1	1	1	1	1	1	1	1	1

NON ORTHURETHRA (Text—Fig.22)

	BM	OC	SC	PS	IL	LR	UR	RR	CC	CPD	CPR	PLD	PLG	VG	PAD	PAG	FG
14SUCCINEIDAE	1	1	1 1	1 1	1 1	3	4	2	2	3	1	1	1	2	2	4	3 1
15ATHORACOPHORIDAE	1	1	1 1	1 2	2 1	5	4	2	3	3	2	2	1	1	2	4	3 1
16ENIDAE	1	1	1 3	1 2	1 2	3	2	1	2	2	1	2	2	1	1	1	2 1
17CHAROPIDAE	1	1	1 3	1 1	1 2	2	2	1	2	2	1	1	1	1	1	1	1 1
18PUNCTIDAE	1	1	1 3	1 1	1 2	3	4	1	3	2	3	2	1	1	2	1	2 1
19DISCIDAE	1	1	1 1	1 1	1 2	2	4	2	3	1	1	1	1	1	2	1	2 1
20ARIONIDAE	1	1	1 1	1 1	1 1	5	4	2	1	2	1	1	1	1	2	3	1 1
21PHILOMYCINAE	1	1	1 1	1 1	1 1	5	4	2	3	3	2	3	3	2	2	3	3 1
23VITRINIDAE	1	1	1 1	1 1	1 2	5	4	2	3	3	3	1	1	2	2	3	1 1
24ZONITIDAE	1	1	1 1	1 1	1 1	1	4	1	3	1	1	1	1	1	1	1	1 1
25PARMACELLIDAE	1	1	1 1	1 2	1 2	5	4	2	1	1	2	1	1	2	2	4	1 1
26MILACIDAE	1	1	1 2	1 2	2 1	5	4	2	3	2	1	1	1	3	2	4	1 2
27LIMACIDAE	1	1	2 1	1 1	1 2	5	4	2	3	2	2	1	1	2	2	4	1 1
29TROCHOMORPHIDAE	1	1	2 1	1 1	1 2	2	4	1	3	3	2	2	2	2	2	2	1 1
30EUCONULIDAE	1	1	1 1	1 1	1 2	2	4	1	3	2	1	2	1	1	2	1	2 1
31HELICARIONIDAE	1	1	1 1	1 1	1 1	1	4	1	3	2	2	1	1	1	2	3	1 1
32FERUSSACIIDAE	1	1	1 2	1 2	1 2	3	4	2	3	2	2	1	1	2	1	3	1 1
33SUBULINIDAE	1	1	1 2	2 1	1 1	1	4	1	3	1	3	1	1	1	1	3	1 1
34ACHATINIDAE	1	3	1 2	2 1	1 1	1	4	2	3	2	3	1	1	2	2	4	1 1
37CLAUSILIIDAE	1	1	1 2	2 1	1 2	3	1	2	1	1	2	1	1	1	1	2	1 1
38OLEACINIDAE	2	1	1 1	1 1	1 1	4	3	2	3	1	2	1	1	3	1	3	1 1
40ACAVIDAE	1	1	1 1	1 1	2 1	3	1	1	2	1	2	1	1	1	1	3	1 1
41BULIMULIDAE	1	2	1 1	1 1	1 1	3	3	2	1	2	2	1	1	3	2	3	1 2
43CERIONIDAE	1	1	1 1	1 1	1 1	3	1	2	2	2	3	1	1	2	1	3	1 1
44UROCOPTIDAE	1	1	1 2	1 1	1 2	3	1	2	3	1	2	1	1	2	2	3	1 2
45SYSTROPHIIDAE	1	1	1 3	1 1	1 2	2	2	1	3	2	2	2	2	1	2	1	2 1
46HAPLOTREMATIDAE	1	1	1 1	1 1	1 1	2	4	1	3	2	3	1	1	2	2	3	1 2
47RHYTIDIDAE	2	1	1 1	2 1	2 1	3	2	2	3	1	2	1	1	2	1	3	1 1

49STREPTAXIDAE	2	1	1 2	1 1	1 2	4	4	2	3	2	2	1	1	2	1	3	1 1
50POLYGYRIDAE	1	1	1 1	1 1	1 1	1	3	1	3	1	2	1	1	2	2	4	1 2
51SAGDIDAE	1	1	1 2	1 1	1 1	1	4	2	3	2	2	1	1	2	2	4	1 2
52CORILLIDAE	1	1	1 1	1 1	2 1	3	1	2	1	1	2	2	1	2	1	1	1 1
53CAMAENIDAE	1	2	1 1	1 1	1 1	1	3	1	3	2	1	1	1	1	2	3	1 1
54AMMONITELLINAE	1	1	1 1	1 1	1 1	3	2	2	1	1	1	1	1	1	1	3	1 1
55OREOHELICIDAE	1	1	1 1	1 1	2 1	3	2	2	1	3	3	2	1	1	2	3	1 1
56BRADYBAENIDAE	1	3	1 1	1 1	1 1	1	4	1	3	1	2	1	1	2	2	4	1 1
57HELMINTHOGLYPTIDAE	1	1	1 1	1 1	1 1	1	3	1	3	1	1	1	1	2	2	4	1 1
58HELICIDAE	1	1	1 1	1 1	1 1	1	3	2	1	1	1	1	1	1	1	3	1 1
=1=	1	1	1 1	1 1	1 1	5	4	2	3	3	2	2	1	1	2	3	3 1
=2=	1	1	1 1	1 1	1 1	5	4	2	3	2	1	1	1	2	2	4	1 1
=3=	1	1	1 1	1 1	1 1	5	4	2	3	3	2	1	1	1	2	3	1 1
=4=	1	1	1 2	1 1	1 1	1	4	2	3	2	2	1	1	2	2	4	1 1
=5=	1	1	1 2	1 1	1 2	3	4	2	3	2	2	1	1	2	1	3	1 1
=6=	1	1	1 1	1 1	1 1	3	4	2	2	2	1	1	1	2	2	4	1 1
=7=	1	1	1 3	1 1	1 2	2	2	1	3	2	2	2	1	1	2	1	2 1
=8=	1	1	1 1	1 1	1 1	5	4	2	1	1	1	1	1	1	2	3	1 1
=9=	1	1	1 1	1 1	1 2	2	4	1	3	2	1	2	1	1	2	1	1 1
=10=	1	1	1 2	1 1	1 1	1	4	2	3	2	2	1	1	2	1	3	1 1
=11=	2	1	1 1	1 1	1 1	3	2	2	3	1	2	1	1	2	1	3	1 1
=12=	1	1	1 1	1 1	1 1	3	3	2	1	2	1	1	1	2	2	3	1 1
=13=	1	1	1 1	1 1	1 1	3	1	2	3	1	2	1	1	2	1	3	1 1
=14=	1	1	1 1	1 1	1 1	3	1	2	1	2	3	1	1	1	1	3	1 1
=15=	1	1	1 1	1 1	1 1	1	3	1	3	1	2	1	1	2	2	4	1 1
=16=	1	1	1 1	1 1	1 1	1	4	1	3	2	2	1	1	1	1	3	1 1
=17=	1	1	1 1	1 1	1 1	3	3	2	1	1	1	1	1	1	2	3	1 1
=18=	1	1	1 1	1 1	1 1	1	4	1	3	1	2	1	1	1	1	3	1 1
=19=	1	1	1 1	1 1	1 2	2	4	1	3	1	1	1	1	1	2	1	1 1
=20=	1	1	1 1	1 1	1 1	3	1	1	2	1	2	1	1	1	1	3	1 1
=21=	1	1	1 1	1 1	1 1	1	3	1	3	1	1	1	1	1	2	3	1 1
=22=	1	1	1 1	1 1	1 1	1	3	1	3	1	1	1	1	1	1	3	1 1
=23=	1	1	1 1	1 1	1 1	3	1	2	1	1	2	1	1	1	1	2	1 1
=24=	1	1	1 1	1 1	1 1	1	2	1	2	1	1	1	1	1	1	1	1 1
=25=	1	1	1 1	1 1	1 1	3	1	2	1	1	2	1	1	1	1	1	1 1
=26=	1	1	1 1	1 1	1 1	3	1	1	1	1	1	1	1	1	1	3	1 1
=27=	1	1	1 1	1 1	1 1	1	3	1	1	1	1	1	1	1	1	3	1 1
=28=	1	1	1 1	1 1	1 1	3	1	1	1	1	1	1	1	1	1	1	1 1
=29=	1	1	1 1	1 1	1 1	1	2	1	1	1	1	1	1	1	1	1	1 1
=30=	1	1	1 1	1 1	1 1	1	1	1	1	1	1	1	1	1	1	1	1 1

APPENDIX G. CHARACTER STATES OF NODES OF TEXT—FIG. 28A

	IL	LR	UR	RR	CC	CPR	PAG
ENDODONTOIDEA	1	2	2	1	2	1	1
ZONITOIDEA	1	1	4	1	1	1	1
CLAUSILIOIDEA	1	3	1	2	1	2	2
HELICOIDEA	1	1	3	1	1	1	3
ACHATINOIDEA	1	1	3	1	2	1	3
ACAVIDAE + RHYTIDIDAE	2	3	1	1	2	2	3
CORILLIDAE	2	3	1	2	1	2	1
OREOHELICIDAE	1	3	2	2	1	1	3
=1=	2	3	1	1	1	2	1
=2=	1	3	1	2	1	1	2
=3=	1	3	1	1	1	1	1
=4=	1	1	3	1	1	1	1
=5=	1	2	1	1	1	1	1
=6=	1	1	1	1	1	1	1